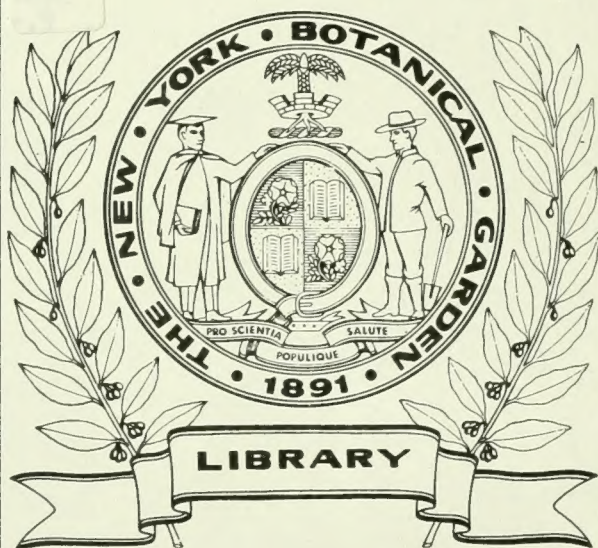


THE NATURAL
HISTORY OF
PLANTS





THE
NATURAL HISTORY OF PLANTS

THEIR FORMS, GROWTH,
REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF
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WITH ABOUT 2000 ORIGINAL WOODCUT ILLUSTRATIONS AND SIXTEEN PLATES IN COLOURS

DIVISIONAL VOLUME V.



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the approach to the floral receptacle open. Dehiscence has already taken place in the case of the anthers of the stamens inserted in front of the sepals, and their pollen is available for cross-fertilization by means of insects, but not for autogamy, owing to the fact that the receptive tissue of the style in the same flower is still inaccessible. (2) The anthers of the stamens inserted in front of the sepals drop off, or else their filaments become reflexed and are exerted beyond the periphery of the flower. The styles move asunder and arrange themselves like the spokes of a wheel in the middle of the flower, where they are liable to be covered with pollen brought by insects from other blossoms. The anthers of the stamens inserted in front of the petals are still closed. (3) Owing to a growth of the erect filaments of the last-mentioned stamens, their anthers are brought to the same height as and in direct contact with the spreading stigmas. Dehiscence ensues, and the liberated pollen is deposited on the receptive stigmatic tissue. In annual caryophyllaceous plants—e.g. in *Silene conica*—the whole process takes place in the course of a single day, whereas in the perennial *Dianthus glacialis* it occupies five or six days, or, if the weather is bad, from seven to nine days.

One of the commonest contrivances for effecting autogamy is the following. Anthers and stigmas stand at the same height, though, owing to the position and direction of the filaments, the anthers are so far from the stigma that no transference of the adhesive pollen to it can take place. At the proper moment, however, the straight and rigid filiform filaments perform certain special movements with the object of conveying pollen from the anthers to the stigma in the same flower. The filaments incline themselves towards the centre of the flower, bringing the anthers into contact with the stigma there situated and pressing the pollen issuing from their loculi on to the receptive tissue. In some plants belonging to this category the displacement of the stamens, which is like the motion of the hands of a clock, is preceded by an elongation of the filaments, and in this respect the plants in question form a transition from those previously described, in the flowers of which autogamy is due to the growth of the filaments. As instances of these transitional forms may be mentioned *Azalea procumbens*, *Draba aizoides*, *Haplophyllum Biebersteinii*, the numerous Saxifrages comprised in the groups of Aizoonia and Tridactylites, and more particularly many Alsineæ and other Caryophyllaceæ. The Saxifrages exhibit a number of individual peculiarities into which we cannot enter in any detail. We must content ourselves with describing two species as representatives of the two groups above referred to, and will select for the purpose *Saxifraga Burseriana*, a plant which grows in the eastern Dolomites, and flowers in early spring, and *Saxifraga controversa* of the group Tridactylites. The flowers of *Saxifraga Burseriana* are protogynous, and the two spreading stigmas are already susceptible of pollination at the time when the petals are only just open, and the anthers are still closed and held near the bottom of the flower on quite short filaments. During this first period of flowering the blossom is adapted to cross-fertilization. Soon afterwards the stamens in front of the sepals lengthen in definite succession, and the anthers,

which meanwhile have undergone dehiscence, are brought to the same level as the stigma. Although the horizontal distance between the stigma and anthers is very small, it is still sufficient to prevent the stigma from becoming coated with pollen from the anthers. Moreover, the stamens standing opposite the sepals incline outwards soon after, thus increasing perceptibly the distance between anthers and stigma. Synchronously with the outward inclination of these stamens there is an up-growth of those which stand in front of the petals, and here again the operation takes place according to a definite law of succession, and continues until the anthers are raised to the height of the stigmas. These anthers, like the others, do not adhere at first to the stigma, and it sometimes happens that the stigma remains unsupplied with pollen even on the sixth day of flowering if none is brought by insects. But, at last, on the seventh or eighth day some, if not all, the filaments move towards the centre of the flower, and the pollen-covered anthers are pressed against the stigma, which has not yet lost the power of receiving the pollen. Usually the five stamens opposite the sepals act in the same manner, and all the ten anthers then ultimately form a ring surrounding the stigma from which pollen may still be transferred by insects to other flowers. The flowers of *Saxifraga controversa* are likewise protogynous, and adapted to cross-fertilization in the first period of flowering. Of the ten stamens, the first to elongate are the five opposite the sepals; the anthers borne at their extremities ascend to the level of the stigma and during the process accomplish their dehiscence. For a short time anthers and stigmas are separated by a small interval of space, but soon afterwards the filaments incline a little towards the centre and deposit pollen upon the stigmas. The five stamens in question then slope away from the centre, and their empty and shrivelled anthers fall off. Meanwhile the five stamens opposite the petals have grown up to the level of the stigmas and offer a fresh supply of pollen for dispersion. But this pollen cannot be used for autogamy owing to the fact that the stigmas shrivel up after they receive the pollen of the first five stamens, and are no longer capable of playing a part in fertilization. The second supply of pollen can, therefore, only be appropriated to the fertilization of younger flowers through the instrumentality of insects. In other words, the five anthers in front of the sepals devote their pollen to autogamy, whilst the five opposite the petals devote theirs to cross-fertilization.

As in these Saxifrages so also in Alsineæ we find two whorls of stamens opposite the sepals and petals respectively, and a certain general resemblance unmistakably exists in the whole arrangement of the various parts of the flowers. The Alsineæ that we here have to deal with are protandrous, and as examples may be taken *Cerastium longirostre*, *Malachium aquaticum*, *Sagina saxatilis*, *Spergula arvensis*, and *Stellaria media*. Dehiscence takes place in the anthers opposite the sepals synchronously with the opening of the corolla, and the pollen exposed thereby is available for cross-fertilization. At that period the styles are still coherent, and the stigmatic tissue, which is composed of short transparent hairs, is inaccessible. Soon afterwards, however, the styles part asunder, and the stigmatic tissue assumes such a position as to ensure cross-fertilization in case insects bringing pollen from other

flowers should visit them in quest of honey. In a short time the stamens opposite the petals raise their anthers to the same height as the stigmatic tissue of the divergent styles; but the filiform filaments slope away from the axis, so that there is always some interval, however small it may be, between anthers and stigmas, and there is still no autogamy. It is not till the last moment, when the flowers begin to close, that the stamens opposite the petals incline towards the centre of the flower, and, laying their anthers upon the stigmatic tissue, cover it with a quantity of their still abundant store of pollen. In most of the Alsineæ, of which we are speaking, the anthers in front of the sepals also come into contact with the stigmas at the same moment, but in a few cases they project above the stigmas and petals, and their pollen is then not available for autogamy. It is remarkable that in the latter, which may be represented by *Sagina saratilis*, the characteristic fact of the pollen of the five stamens opposite the sepals being devoted to cross-fertilization, and that of the five stamens opposite the petals to autogamy, is exactly the reverse of the arrangement found to exist in the Saxifrages above described.

Next to this series of plants of which the Saxifrages of the Aizoonia and Tridactylites groups and the Alsineæ above-named are the chief representatives, comes another composed predominantly of Cruciferae. They are for the most part annual species with small flowers, which are but little visited by insects, and the majority of their fruits must be looked upon as products of autogamy. *Cochlearia Greenlandica*, *Draba borealis*, *Draba verna*, *Clypeola Messanensis*, *Lobularia nanumularia*, *Hutchinsia alpina*, *Schierckia Podolica*, *Lepidium Draba*, *Alyssum calycinum*, are a few examples, and the selection shows incidentally that the range of the cruciferous plants in question extends from the extreme North to the latitude of the Sahara, and from high altitudes to the level of the deep-lying steppes: in fine, that this same process of autogamy recurs under the most diverse external conditions. All these Cruciferae are protogynous, and have six stiff stamens, four long and two short. The anthers of the former are still closed when the flower opens, but are already on the same level as the stigma. Autogamy is, however, prevented immediately on the dehiscence of the anthers, owing to there being a little horizontal interval between them and the stigma. It is not till the flower is almost over that the erect filaments move sufficiently towards the middle of the flower to deposit the pollen upon the stigma. The pollen of the shorter stamens does not get transferred at all to the stigma in the same flower except in a few species. It is carried away by insects and used for cross-fertilization, whilst the pollen of the longer stamens mainly subserves the purpose of autogamy. *Lepidium Draba* exhibits a curious contrivance to prevent the four longer stamens from being touched by insects and despoiled of their pollen during the first part of the time that the flower is open. The stamens referred to bend outwards and hide themselves for a time behind the petals. The advantage of this movement is that in no circumstances can there be a deficiency of pollen for the ultimate process of autogamy. In *Hutchinsia alpina* usually only one of the four longer stamens approaches sufficiently near to the stigma to cover it with pollen, and after it has effected this object, it removes

itself again away from the axial position. All these movements are performed as a general rule with great rapidity. In *Alyssum calycinum* they take a few hours, in *Draba verna* the interval between morning and evening.

Some annual species of the Wood-sorrel genus—such as *Oxalis stricta*, for example—have five short and five long stamens in each flower. The anthers of the latter are of the same height as the stigmas, but begin by being at a little distance from them, so that at this period cross-fertilization may be effected by insects alighting upon the stigmas. Within the space of a few hours, however, the longer stamens incline towards the stigmas and deposit their pollen upon them. Here, again, the pollen of the five shorter stamens does not reach the stigma in the same flower, but is devoted to cross-fertilization. As in these annual species of Wood-sorrel, so also in the majority of species of St. John's-wort (*Hypericum*), the unequal length of the stamens, combined with the fact of the non-simultaneity of sexual maturity (*dichogamy*), is of advantage to the plant in that it ensures that autogamy shall take place just before the flower fades, whilst permitting at an earlier period cross-fertilization by the pollen of other flowers through the agency of insects. In *Hypericum perforatum*, which may be chosen as our example, the pistil is encompassed by a number of filiform filaments of unequal lengths, so arranged that the longest are in close proximity to the central pistil and the shortest near the periphery of the flower. The anthers do not liberate their pollen simultaneously, but one group does so after another. Dehiscence takes place first in the short stamens, next in those of median size, and last of all in the long ones. As soon as an anther opens, the filament bearing it inclines inwards, and thus one after another, the short, median, and long filaments stand up and approach the middle of the flower. It being only the anthers of the longest stamens that are on the same level as the stigmas, autogamy cannot occur till quite at the last, not long before the flower withers.

The widely-distributed Star of Bethlehem (*Ornithogalum umbellatum*) exhibits on the opening of the flower six stamens arranged in two whorls with three in each whorl. The stamens of the inner whorl are the longer, and their anthers dehisce a day sooner than the others. All six filaments look erect in the newly-opened flower, but are really sloped slightly outwards, with the result that the anthers are separated by an interval of about 3 mm. from the small stigma in the middle of the flower. So long as they maintain this position the pollen cannot be directly deposited upon the stigma, and the aim of the flower at this stage is to secure cross-fertilization through the intervention of honey-seeking insects. Towards the end of the flower's period of bloom both the long and the short stamens approach the centre, but only the anthers of the three shorter ones are applied to the stigma and besmear it with pollen; the other three do not come into contact with the stigma owing to their standing at a higher level. Thus the Star of Bethlehem differs from the cases previously described in that it devotes the pollen of the shorter stamens to autogamy and those of the longer stamens to heterogamy (cross-pollination). This is partly due to the circumstance that the anthers of the three longer stamens

are placed just in front of the approach to the nectaries of the ovary and in such a position are certain to be brushed by insects, whilst no honey is to be found behind the anthers of the three shorter stamens, and insects, therefore, make no attempt to enter past them. These anthers, consequently, retain their pollen, and when the flower is nearly over yield it up for the purpose of autogamy.

A curious contrivance is exhibited by *Aphyllanthes Monspeliensis*, a plant indigenous to Southern Europe. Like the Star of Bethlehem, it has three long and three short erect stamens in each flower, and the anthers are not at first in contact with the stigma. But before the final closing of the perianth all the stamens slope towards the stigma, which is subdivided into six lobes, three at the top and three lower down, so that the pollen of the three shorter stamens is deposited on the lower stigmatic lobes, and soon afterwards that of the three longer stamens is deposited on the three upper stigmatic lobes.

In many plants where all the stamens are of the same length, and where the anthers are already on the same level as the stigma at the time when the flower opens, the process of autogamy is essentially identical with that above described. The anthers are held by erect filaments at a little distance from the stigma, but later on, after various movements have been accomplished by the filaments, they adhere to the stigma and deposit their pollen upon it. This is the case, for instance, in *Paris quadrifolia*, in several species of *Scilla*, in *Chelidonium* and *Ranunculus*, in *Samolus Valerandi*, in *Androsace elongata*, *A. maritima* and *A. septentrionalis*, in *Lysimachia nemorum* and in *Swertia perennis* and *S. punctata*. It is not possible here to discuss all these plants individually, and only a few points in connection with them will be referred to. In the Herb Paris (*Paris quadrifolia*) the period during which each flower remains open is very long. The stiff stamens at first stand out radially, but later they describe an angle of 80° towards the middle of the flower, where they converge over the pistil and press their anthers upon the stigmas. In the plants of the order Primulaceæ—viz. *Samolus Valerandi*, *Androsace elongata*, *A. maritima*, and *A. septentrionalis*—the corolla is salver-shaped, and the short filaments, which are adnate to the tube of the corolla, only need to incline slightly towards the axis in order to transfer their pollen to the stigma in the same flower. The majority of these plants are protogynous: the flowers of *Swertia perennis* and *S. punctata* alone are markedly protandrous. There is, therefore, in the case of the latter no chance of cross-fertilization at the beginning of the period of flowering, the stigma being still closed. On the other hand, pollen is available for transport by insects to flowers that happen to be at a later stage of development. The next step is for the stigma to open and so dispose its two lobes that flies arriving with a supply of pollen from younger blossoms are obliged to effect cross-fertilization. To prevent restriction or frustration of this process of heterogamy, and also to ensure the preservation of some pollen for autogamy in the opposite case of an absence of insect-visitors, the five stamens bend outwards simultaneously with the opening of the stigma, exerting their anthers and hiding them under the stellately-expanded petals. If no insects come, and cross-fertilization is therefore

excluded, the filaments straighten themselves again and then move like the hands of a clock towards the middle of the flower, where they press their anthers, which still retain a little pollen, upon the stigma.

The stamens, which are instrumental in effecting autogamy by movements of inclination in the direction of the stigma, are straight at the commencement of the period of flowering in all the plants above enumerated. Sometimes they curve

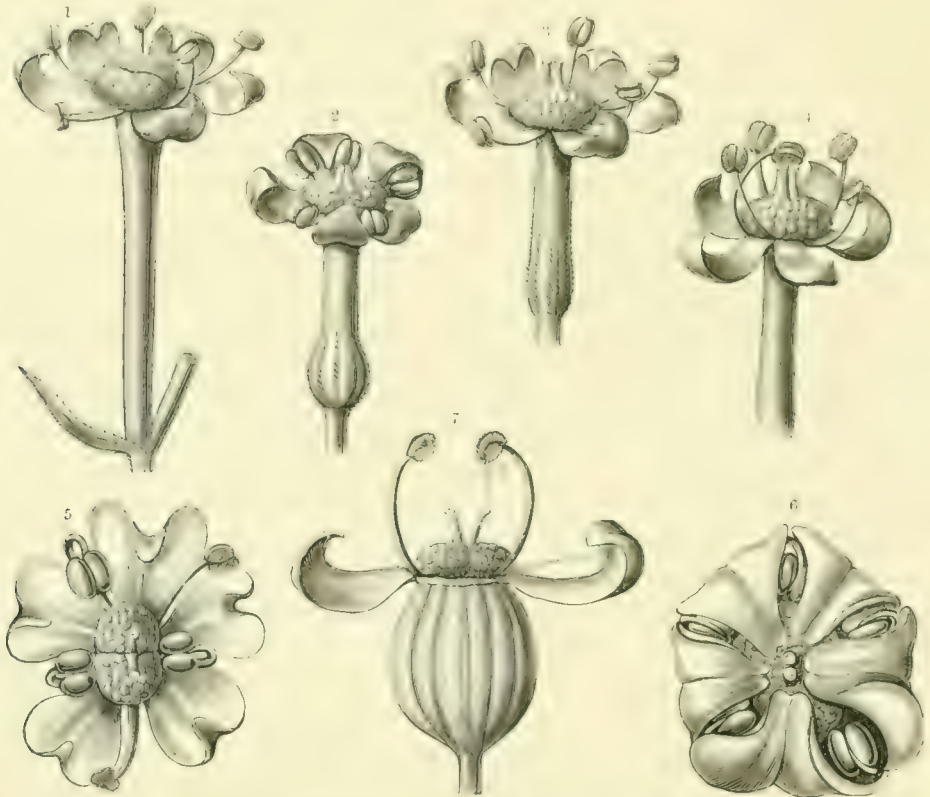


Fig. 296.—Autogamy effected by the inclination of curved stamens.

1 Pseudo-hermaphrodite male flowers of the Venus' Comb (*Scandix Pecten-Veneris*). 2, 3, 4 Successive positions assumed by the true hermaphrodite flowers of the Venus' Comb at first with a view to cross-fertilization, afterwards with a view to autogamy. 5, 6, 7 Successive positions assumed by the true hermaphrodite flowers of the Fool's Parsley (*Ethusa Cynapium*) at first with a view to cross-fertilization, afterwards with a view to autogamy. All the figures magnified.

outwards for a short time, but before the flower fades, and particularly at the moment of autogamy, they are invariably erect again.

There is, however, another group of plants to be considered in which the filaments are already inflexed in the bud, and continue so at the time when pollen from the anthers at their extremities is deposited upon the adjacent stigmas. The most important examples of plants exhibiting this autogamy by means of an inclination of inflexed filaments are afforded by several annual Umbellifers with protogynous flowers (*Ethusa Cynapium*, *Caucalis daucoides*, *Scandix Pecten-Veneris*, *Turgenia latifolia*, &c.). Two kinds of flowers are associated together in the umbels of the Venus' Comb (*Scandix Pecten-Veneris*; see fig. 296^{1, 2, 3, 4}),

namely, pseudo-hermaphrodite (*cf.* p. 294) male flowers (fig. 296¹) and true hermaphrodite flowers (figs. 296^{2,3,4}). The latter open earlier than the former, which, indeed, never come into play until the hermaphrodite flowers have cast both stamens and petals. Directly the petals open in the hermaphrodite flowers a finely-granulated honey-secreting disc and two short styles are revealed in the middle of the flower. The stigmas at the extremities of the styles are already mature, but the stamens are incurved like hooks and have their anthers still closed (fig. 296²). The day after, also, when the petals have opened further back and



Fig. 297.—Autogamy effected by inclination of curved stamens.

¹ *Cirsia alpina*. ² A newly-opened flower of *Cirsia alpina* with the front petal removed. ^{3, 4} The same flower at a later stage of development. ⁵ Fruit of *Cirsia alpina*. ⁶ *Agrimonia Eupatoria*. ^{7, 8, 9, 10} Successive phases of a flower of *Agrimonia Eupatoria*, which is at first adapted to heterogamy (cross-pollination) and subsequently to autogamy. ¹¹ Young fruit of *Agrimonia Eupatoria*. ^{1, 6, 11} natural size; the rest of the figures magnified.

the filaments have straightened out (fig. 296³), the anthers surrounding the stigma in a circle are still closed, so that pollination can only take place at this period in the event of insects bringing pollen from other flowers. The anthers and filaments have, however, now entered upon an active phase. The curved stamens bend successively at short intervals, one after the other (after one has started, the next to follow is the stamen next but one to the left, and so on till all have done) towards the centre of the flower, bringing their anthers, which have meanwhile undergone dehiscence and are covered with pollen, into contact with the stigmas precisely in the manner shown in fig. 296⁴. Each stamen only stays a short time in this position, and then executes a backward movement and makes way for the next in order. When all the stamens have accomplished these evolutions, they as well as the petals become detached and fall to the ground. The secretion of honey

on the rough surface of the pad of tissue in the middle of the flower ceases, the pollinated stigmas turn brown, and the period of bloom for that particular flower comes to an end. The imperfect staminiferous flowers do not unfold until all the hermaphrodite flowers are over, a fact which can only be interpreted as indicating that their pollen is to be devoted to the fertilization of protogynous hermaphrodite flowers of other individuals which are still in the first stage of flowering. Fool's Parsley (*Æthusa Cynapium*, see figs. 296^{5, 6, 7}) differs from the Venus' Comb and the other annual Umbellifers above referred to in that all the flowers of an umbel are hermaphrodite, and that the filaments, which in the bud are tucked in like springs (fig. 296⁵), not only straighten out when the flower opens, but elongate, and thus raise the anthers to a higher level than the stigma. Also in Fool's Parsley, as has been mentioned before, the anthers are not laid right against the stigmas, but remain a little higher, and let their pollen fall upon them from above (see fig. 296⁷). This at least is what I saw in the case of the common Fool's Parsley or *Æthusa Cynapium*; the small *Æthusa segetalis*, on the other hand, according to my observation, much more frequently brings its anthers into contact with the stigmas in the same manner as the Venus' Comb (see fig. 296⁴).

Autogamy of the same type as that described in the above instances of annual Umbelliferae also takes place in many small-flowered Bed-straws (e.g. *Galium infestum*, *G. Mollugo*, *G. tricornis*), in the Dodder (*Cuscuta*), in the Alpine Enchanter's Nightshade (*Circæa alpina*), and in Agrimony (*Agrimonia Eupatoria*). Of the Enchanter's Nightshade (see figs. 297^{1, 2, 3, 4}), it is only needful to note that the number of stamens is limited to two, and that sometimes one anther alone is laid upon the stigma (297³), but not infrequently both subserve the purpose of autogamy in that manner (297⁴). In the latter case the stigma looks as if it were grasped by the two limbs of a pair of tongs. The flowers of Agrimony have from 12 to 20 stamens, and are protogynous. The anther-filaments are very slightly incurved, each corresponding to about a sixth part of the circumference of a circle (fig. 297⁷), but as soon as dehiscence takes place the filaments bend one after another towards the centre of the flower (see fig. 297⁸) until they are in the form of semicircles, and some of the anthers covered with pollen come into direct contact with the stigmas, which are still in a receptive condition (fig. 297⁹). Soon after the stigmas have thus been furnished with pollen the anthers drop off the filaments, and the latter coil up still more as is shown in fig. 297¹⁰.

Several species of Stonecrop (e.g. *Sedum annuum*, *S. atratum*, *S. dasycphyllum*), and some House-leeks (e.g. *Sempervivum montanum*, *S. Ruthenicum*) have two kinds of stamens in each flower, namely, those inserted in front of the sepals and those inserted opposite the petals. The anthers of the former are the first to open, and as they are quite close to the stigmas only a slight inclination of the curved filament is necessary to bring about autogamy. After a deposition of pollen upon the stigmas has already taken place, the filaments opposite the petals also curve over inwards, and the anthers, which meantime have undergone dehiscence, are held right over the stigmas. But, seeing that the latter are by this time withered

and have no further need of pollen, we are bound to infer that this fresh supply is offered for the purpose of effecting by insects' aid the fertilization of other flowers in which there is as yet no available pollen although the stigmas are accessible and mature. *Opuntias* and all the numerous species of the Rose genus (*Rosa*) behave in a similar manner. In them also some of the anthers devote their pollen to autogamy, whilst the others devote theirs to cross-fertilization. The filiform filaments are curved and of unequal lengths. The anthers borne by the innermost whorl of filaments open first, but their pollen is of no use for autogamy, notwithstanding the proximity of the stigmas, because the anthers are lower than the stigmas and do not spontaneously come into contact with them. Only the filaments of the outermost whorl are of the right length, and these alone curve over and lean towards the middle of the flower until their anthers rest immediately upon the stigmas. As, however, these anthers are the last to dehisce, autogamy does not ensue till the very last moment of flowering; for the whole of the time up till now the flower is adapted to cross-fertilization only.

In a number of *Ranunculaceæ*, such as *Anemone Hepatica*, *A. Transsylvanica*, *Ranunculus alpestris*, *R. acer*, and *R. montanus*, the structure of the flowers resembles to a certain extent that of Roses. A group of pistils with short styles and almost sessile stigmas rises up in the middle of the flower, and is surrounded by a large number of stamens which are arranged in several whorls and are in their turn encompassed by the petaloid sepals. The flowers are protogynous, and at the commencement of their period of bloom can only undergo cross-fertilization through the agency of insects. At a subsequent stage also after the dehiscence of the anthers of the outer whorl and the exposure of their adhesive pollen, the flowers are still adapted to heterogamy: for the distance of these anthers from the stigmas is comparatively great, and insects always alight on the group of carpels in the centre and make their way from them over the anthers to the circumference, whence they again take flight in order to visit another flower. But by degrees the stamens of the inner whorl also mature: the filaments, which hitherto have been very short, grow considerably and curve inwards, laying upon the stigmas their anthers which have meanwhile burst open. The sepals of these *Ranunculaceæ* close up when it begins to get dark, and the flowers assume a nodding position owing to a slight inflection of their pedicels. It might be supposed that these movements also are accessory to autogamy, and, as a matter of fact, in many other *Ranunculaceæ*, which will be the subject of discussion later on, such co-operation does occur; but, in the *Anemones* and *Ranunculuses* above referred to, no supplementary action of the kind is necessary, and the closing and nodding of the flowers in wet weather and during the night are resorted to merely with the object of protecting the pollen from moisture.

To this long list of plants with protogynous flowers must now be added a few protandrous species from the genera *Gypsophila*, *Saxifraga*, and *Cuphea*. The flower of *Gypsophila repens* contains ten stamens, of which five are inserted in front of the sepals and five in front of the petals. In the bud they are all tucked in like

hooks; in the open flower they are straight and slope outwards. Contact with the central stigmas, which meanwhile have become mature, is impossible so long as the stamens maintain the latter position; but shortly before the flower fades, the stamens become inflexed, and their anthers are thus brought against the stigmas. The *Saxifragas* also have two circles of stamens in each flower. In the species of the sub-genus *Cymbalaria* (*Saxifraga Cymbalaria*, *S. Huetiana*, &c.), the first to straighten out are those standing opposite the sepals. Their anthers open and display their pollen at a time when the adjacent stigmas are closed together, and are not as yet capable of taking up pollen. This supply of pollen is not therefore used for autogamy, but is obviously available for crossing with other flowers. After exposing their pollen one after another in definite order for a couple of days, these stamens incline outwards and let their anthers fall. The styles, now, for the first time, move asunder, and their stigmas become capable of receiving pollen. As the anthers of the stamens opposite the sepals have dropped off, and those of the stamens opposite the petals are still closed, the stigmas are only liable at this stage in the development of the flower to be dusted with pollen from other flowers or other plants. Eventually signs of vitality are also exhibited by the stamens opposite the petals. They become strongly inflexed, their anthers dehisce, and, the stigmas being still receptive, the period of the flower's duration is brought to a close by the anthers being pressed against the stigmatic surface and effecting autogamy. The same sort of thing is observed in the case of the protandrous flowers of several species of the genus *Cuphea*, as, for instance, in *Cuphea eminens*. These flowers, of which mention has already been made on p. 235 (figured on p. 237), face sideways and contain eleven stamens of varying length whose anthers are disposed in two irregular rows above the expanded calyx-tube. The style is short at the commencement of flowering, and is concealed, together with the immature stigma, underneath the anthers. Dehiscence occurs on the upper faces of the anthers which are turned away from the style, and the pollen issuing from the sutures is fated by its position to be rubbed off by honey-sucking insects, and to be eventually used for cross-fertilization. Two days later the style, which has in the meantime increased in length some 11 mm., projects above the stamens, bringing the stigma into the line of entrance to the honey (fig. 262², p. 237). Should insects now visit the flower, bringing with them foreign pollen, cross-fertilization is certain to ensue. But, in the event of an absence of insects, the longest stamen bends up to the stigma and presses that face of the anther which is coated with pollen against the stigma.

The degree of inflection of the filaments in the cases hitherto described scarcely corresponds to the third of the circumference of a circle, and is but seldom actually spiral. But that more pronounced movements of inflection do occur for the purpose of effecting autogamy, is shown by the case of *Nicandra*, a plant belonging to the Solanaceæ, and that of *Calandrinia compressa*, belonging to the order Portulacæ. In *Nicandra* the long filaments bend down to the extent of at least a semicircle to reach the stigma in the event of a failure of pollen from extraneous sources, and in the ephemeral flowers of *Calandrinia compressa*, the filiform filaments curve

gently away from the velvety stigma at 9 A.M., *i.e.* shortly after the expansion of the petals, whilst three or four hours later, when the petals close up again, they undergo spiral inflection from right to left and lay their anthers upon the stigmas.

The cases in which the stigmas are the agents in the operation of transfer to themselves of pollen from the anthers of the same flower may be classed in two divisions, (1) those in which a direct contact between the stigma and the anthers is effected by some definite bending or other movement of particular parts of the pistil; and (2) those in which the pollen is first deposited by the anthers and stored in some part of the flower other than the stigma; ultimately the stigmatic tissue is brought in contact with it in the same manner as in (1), *i.e.* by some movement on the part of the pistil.

The cases comprised in the first division fall naturally into four groups.

To the first group belong all those in which autogamy is produced by *contraction* of the style. The Cactiform plants of the Mexican plateaux, in particular, various species of the genera *Cereus*, *Echinopsis*, and *Mammillaria*, exhibit in their flowers a number of filiform stamens, arranged in a close spiral around the passage leading to the honey secreted on the floral receptacle. In the midst of this thicket of stamens stands a long style which terminates in a stellate stigma. The anthers are already covered with pollen when the petals unfold, but the stigma, which projects considerably beyond the anthers, is still closed, its fleshy lobes being coherent and forming a kind of club, so that there can be no possibility of its being dusted with pollen. Thus the flowers are markedly protandrous, and the pollen liberated during the first part of their period of bloom can only be used for cross-fertilization. The next step is the opening of the stigma and spreading out of its lobes into a star in front of the entrance to the nectary. Insects now alighting are obliged to brush against the stigma before they can get at the nectar, and in so doing they deposit a portion of the store of foreign pollen with which they are laden upon the stigma and initiate a process of cross-fertilization. This stage may last a few hours only, or several days, or over a week, according to the species. When the term of the flower's duration is nearly reached the style contracts in length, and the stigma, which has hitherto been above the anthers, is drawn into the midst of them, so that it cannot fail to get covered with the pollen, of which there still remains a quantity clinging to the anthers. In *Cereus dasycanthus* the stigma soon after the opening of the flower projects 1 cm. beyond the anthers. The length of the style bearing the stigma is at that time 20 cm. When the flower is nearly over, the style is only 16.5 cm. long, and the stigma is therefore drawn in through a space of 3.5 cm. and no longer surmounts the stamens, but, on the contrary, is 2.5 cm. lower than the anthers of the longest stamens.

The second group includes all cases where autogamy is brought about by an *elongation* of the ovary or the style. *Epimedium alpinum*, a native of the warm valleys of the Southern Alps, has four sepals arranged crosswise and beneath these—the flowers being partially inverted as shown in figs. 298^{1,2,3}—four petals fashioned like little slippers and containing an abundance of honey in their blunt

saccate interiors. The ovary is spindle-shaped, and bears at the end of a short style a stigma covered with little papillæ. The stamens, four in number, rest with their dorsal surfaces in contact with the ovary; their anthers face outwards, are lanceolate in shape, and each carries on its apex a small foliaceous scale like the point of a spear (see fig. 298⁴). The flowers are protogynous, or, in other words, the papillose stigma, which is hemmed in by the four scales just referred to, is already mature at a time when the anthers are still closed (fig. 298¹). At this stage the stigma may be dusted with pollen from other flowers. The next step is the dehiscence of the bilocular anthers, which takes place in a very peculiar manner. The wall of each anther-half which faces outwards becomes detached, and is lifted up in the form of a flap with the whole of the pollen of the corresponding cavity sticking to its inner surface. The two flaps then shrivel and roll up, with the originally internal surface outside, until the only point of attachment is just below the pointed scale at the apex of the anther; the free flaps arch over this foliaceous anther tip (fig. 298⁵), and also over the stigma, which is close to the scale (fig. 298²). The process is simultaneous in all four anthers, the result being that the stigma is roofed over by a vault composed of eight curved flaps, and as the exposed surfaces of the latter are thickly coated with pollen, the whole arch presents externally a continuous covering of that material (see fig. 298²). Should insects now visit the flower to obtain the honey stored in the slipper-shaped petals they must brush past this pollen-covered vault; nor can they fail to be besmeared at the very spot where at a previous stage in the flower's development they would have had to brush against the stigma. This condition of affairs lasts usually for two days. In the meantime changes affecting the pistil are taking place which, notwithstanding their inconspicuous nature, are of the greatest importance in relation to the eventual accomplishment of autogamy. If the stigma is not dusted by insects with foreign pollen at the first expansion of the flower the pistil now elongates sufficiently to raise the stigma into the vaulted cavity just described: and as the flaps composing the vault curl up still more (fig. 298⁶) as the flower approaches its end, the stigma must inevitably come into contact with the pollen adherent to them (cf. fig. 298³).

A similar process is observed to take place in several Cruciferæ, of which the Charlock (*Sinapsis arvensis*) is a typical instance. The flowers of this plant are protogynous. The bud opens early in the morning, revealing still closed anthers with their faces turned inwards (*introrse*), whilst the stigma is already mature and projecting somewhat above the anthers. At this stage of development no pollen except what is brought by insects can be deposited on the stigma. A day later the flower presents quite a different appearance. The four longer stamens have stretched and curved a little away from the axis, and the anthers are lifted above the stigma. By a rapidly executed twisting of the filaments the anthers have been turned round so as to face outwards, and extrorse sutural dehiscence has meantime taken place. The stigma is completely withdrawn from observation, and is also safe from any possibility of being dusted with pollen, for the anthers in the same flower have turned away their pollen-coated faces, nor is it possible for any extraneous pollen

that may happen to be brought by insects to be transferred to the stigma, owing to the anthers forming a hood over it. At this stage every other object is subordinated to the dispersion, through the agency of insects, of the pollen exposed by the flower. After the interval of another day the observer finds a third aspect of the flower presented to him. The filaments have straightened themselves out, and so brought the anthers nearer to the stigma; the coating of pollen has spread all over the anthers,

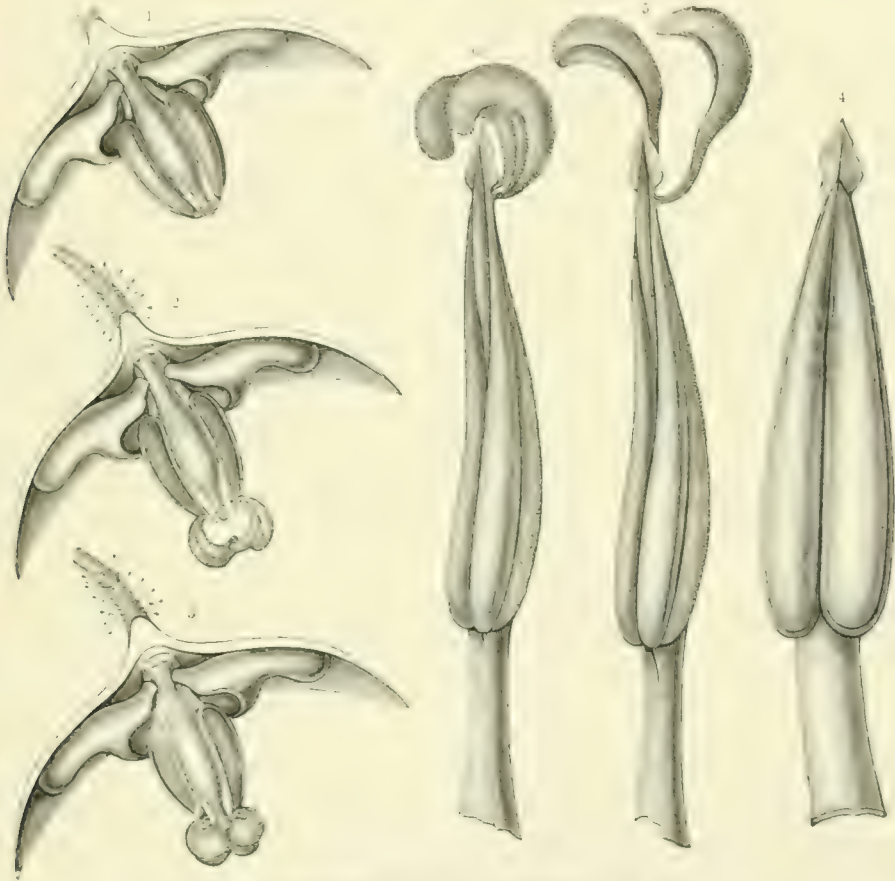


Fig. 298.—Autogamy brought about by elongation of the pistil.

1, 2, 3 Flower of *Epimedium alpinum* at successive stages of development, showing primary adaptation to cross-fertilization and subsequent adaptation to self-fertilization. 4 Front view of a closed anther. 5 Side view of the same. The front (right-hand) wall of each of the two loculi has become detached and been raised up as a flap or valve. 6 The same anther; the flap has curled up more tightly and now forms a sort of cowl arching over the spear-like apex. 1, 2, 3 $\times 10$; 4, 5, 6 $\times 25$.

and the ovary has undergone elongation, carrying the stigma into the midst of the dome of anthers, where it becomes thickly overlaid with pollen

Again, in the nodding flowers of *Atragene alpina*, and in these of *Clematis integrifolia*, which grows freely in the swampy meadows of the Hungarian plains, we find autogamy effected by means of an advance of the pistil into proximity to the anthers laden with pollen. Both plants are protogynous—the stigmas being mature for a short time before the anthers dehisce—and in both the newly-opened

flowers are adapted to cross-fertilization. The stamens lie one upon another like the tiles of a roof, and together form a short tube at the bottom of which are a number of closely-clustered carpels, whilst at the free edge of the tube the anthers expose their store of pollen. The first anthers to open are those pertaining to the outermost and longest stamens, the next belong to those of median length, and the last to the shortest, which are in the immediate vicinity of the carpels. The pollen of the outermost anthers serves mainly for cross-fertilization, and can hardly ever be used for autogamy on account of its position; but even in the case of the latest anthers belonging to the shortest stamens, no pollen could reach the stigmas were it not for the elongation of the carpels, which occurs during the last two days of the flower's duration. The anthers still contain pollen at this late period, and a quantity adheres, besides, to the silky hairs clothing their filaments, so that the slightly divergent stigmas get covered with an abundant supply of pollen as the carpels lengthen and push them up through the pollen-coated tube (see fig. 246³, p. 174).

The flowers of the Lady's Mantle (*Alchemilla vulgaris*) are likewise protogynous. When a flower opens, the anthers of the four short stamens are still closed, whilst the stigma is already mature, and is seen in the middle of the flower projecting through and slightly above a kind of diaphragm which is stretched across the floral interior and secretes honey. At this stage cross-fertilization alone is possible; but in the course of twenty-four hours the style grows in an oblique direction, until its extremity bearing the stigma strikes against one of the four anthers, which have meanwhile undergone transverse dehiscence; it thus receives a sprinkling of pollen (see fig. 226⁵, p. 125). The pollen of the three other anthers is still available for transference by flies to the stigmas of other flowers.

The above are a few instances of the methods in which autogamy is effected by elongation of the style or of the entire pistil. Taken generally this process must be classed among the rarer forms of the phenomenon, though it is surprising that it should be so considering the frequency of autogamy by means of the elongation of stamens. The accomplishment of autogamy through the *inclination* of a style otherwise straight is of even less usual occurrence. The most striking example of this process is afforded by the bilabiate flowers of the North American *Collinsonia Canadensis*. In the newly-opened blossom the long style stands midway between two exserted stamens which are almost as long as the style. Towards the end of the flower's period of blossom, the style begins to slope towards one of the stamens, moving like the hand of a clock through an angle of from 20° to 40° until its stigma comes against the pollen-covered anther borne by the stamen in question.

A much more common method of bringing about autogamy is for parts of the pistil—usually the style—to bend so as either to bring the stigmas into direct contact with the anthers belonging to the same flower, or to place them in such a position beneath the anthers as to ensure their catching any pollen that may fall out of the loculi. The direction of the style's inflection depends upon the form and mode of insertion of the flower, and more particularly on the position assumed by the anthers. The flowers of the Great Mullein (*Verbascum Thapsus*), of the Corn-

salad (*Valerianella Auricula*, *V. carinata*, &c.), and of the non-twining species of Honeysuckle (*Lonicera alpigena*, *L. nigra*, *L. Xylosteum*) are protogynous, and the style is so placed when the corolla opens that its stigma must of necessity be brushed by insects as they make their way to the receptacle. There is evidently at this stage no possibility of any but cross-fertilization. Later on, when the anthers open and expose their pollen, the stigma is taken quite out of the way, the style becoming bent downwards or to one side, so that the stigma cannot come into contact with anthers of the same flowers either spontaneously or through the agency of insects. Not till the flowering period is nearly over does the style return to its original position; when this happens, the stigma is raised by the straightening up of the style, and is pressed against the anthers, which are still coated with pollen. The flowers of the Martagon Lily (*Lilium Martagon*) are nodding, and have their



Fig. 299.—Autogamy effected by means of an inflection of the style.

¹ Flower of *Tricyrtes pilosa* in the first stage of its development. ² The same in the last stage of development. ³ Flower of *Morina Persica* in the first stage of development. ⁴ The same in the last stage of development. ⁵ Stigma of *Morina* covered with pollen from anthers belonging to the same flower. ⁶ Flower of *Euphrasia minima* in the first stage of development. ⁷ The same in the last stage of development. All the figures slightly magnified. In figs. 2, 3, 4, 6 and 7 the front part of the flower is cut away

perianth-lobes strongly reflexed. In each petal there is a groove which is roofed over and closed in the middle by two coalescing rims, so that the honey stored in the groove can only be sucked out by insects at the two extremities where the groove is open. The flowers are protogynous, and, when they are newly open, the style is straight and holds its stigma in such a position that it is sure to be touched by insects sucking honey from the inner orifice of the groove. As the anthers are still closed at this stage, only foreign pollen can be affixed to the stigma. Subsequently dehiscence ensues, and the position of the anthers in front of the external orifice of the groove ensures their pollen being brushed off by insects trying to suck the honey at that end, whilst the stigma is left untouched by them. In this second stage of the flower's development the style begins to bend a little to one side, and, towards the end, the curvature increases to such an extent that the stigma comes into contact with one or sometimes two of the anthers, and dusts itself with pollen. Often enough, it is true, the stigma misses its mark, and in consequence autogamy is not so certain to occur in the Martagon Lily as in most of the other cases. It

must also be noted that the inflection of the style only takes place should the stigma have not previously been supplied with extraneous pollen. If there has been cross-pollination at the commencement of flowering the inflection either does not occur at all or is so trifling as to be of no significance.

The transference of pollen to the stigma by means of a bending down of the style is observed in various species of *Tricyrtes*, *Morina*, *Oenothera*, and *Epilobium*, in several Rhinanthaceæ, Caryophyllaceæ, and Ranunculaceæ, and in most of the Malvaceæ. The flowers of *Tricyrtes pilosa*, of which figures are given above, are protogynous. Each of the three styles is bent down, and has a bifurcated extremity, so that it looks not unlike a claw. The stigmatic tissue is situated at the end of the claw, and is brushed by insects on their alighting to suck honey from the saccate bases of the perianth-segments. The free extremities of the filaments curve down in semicircles, and the anthers are suspended under the claws of the style (fig. 299¹). At the time when the anthers have their pollen exposed they are so situated as to stand in the way of insects coming in quest of honey. Without the assistance of insects there could be no transference of pollen to the stigma so long as stigmas and anthers remained in the same relative positions, and the flower remained upright. But the chance of insects not visiting the flower is provided for by a downward bending of the claws of the style, which continues until the stigmatic tissue at their extremities comes into direct contact with the pollen-coated anthers (see fig. 299²).

The process above described takes place in the course of a week in *Tricyrtes pilosa*, but in *Morina Persica*, one of the Dipsaceæ (see figs. 299^{3, 4, 5}), it is all accomplished within a few hours. The difference between the times at which stigmas and anthers respectively attain maturity in *Morina* is scarcely half an hour, but even this short interval suffices to render cross-fertilization possible during the first stage of flowering, whilst in the second stage autogamy obtains. All the species of the genus *Morina*—including *Morina Persica*, the type here selected for illustration—unfold their flowers at dusk. As soon as the corolla-limb expands the thick pulvinate stigma becomes visible in the middle of the flower just above the entrance to the honey. The receptive tissue is on the upper surface of the stigma. The two anthers are stationed behind the stigma, and when insects insert their probosces into the long honey-filled tube of the corolla they are certain to effect cross-fertilization, provided they have previously visited flowers at a somewhat later stage of development. In the case of other plants whose flowers open in the morning it would be scarcely likely that insects should alight immediately after the opening of the passage to the honey, but the flowers of *Morina* are adapted to crepuscular and nocturnal moths, which only have two or three hours of darkness in which to get the honey, and must, therefore, make great haste and employ the whole of the time if they are not to fail in their quest. As a matter of fact the moths in question leave their haunts within a quarter of an hour of the time when the flowers of *Morina* open, and one may be sure that wherever Sphingidæ and Noctuæ with probosces 3 or 4 centimetres in length abound, one or more will come flying to suck the honey as soon as the floral receptacle becomes acces-

sible. Thus, dichogamy, involving hardly half-an-hour's interval between the attainment of maturity in stigmas and anthers respectively, is sufficient to ensure cross-fertilization at the commencement of the period of bloom in each flower of this kind of night-flowering plant. A further adaptation with a view to heterogamy is shown in the position of the stigma in front of the anther in the first stage of floral development (see fig. 299³). On the intrusion of insects—Sphingidæ, Noctuæ, &c.—into the interior of the flower the large stigma is the first object encountered, and next to it come the anthers, and there is therefore a possibility that even during the time that the anthers are open and have their pollen exposed cross-fertilization may take place through the agency of insects. If, however, no insects visit the flower the style bends down the very next morning in an open curve and lays the stigma flat upon the anthers (see fig. 299⁴). The pollen readily adheres to the surface of the stigma, as may be seen by removing that organ after it has become appressed to the anthers, when a thick layer of pollen will be found sticking to it (fig. 299⁵).

Inflections of the style in all respects similar to those exhibited in *Morina* occur in the flowers of numerous Rhinanthaceæ, e.g. in *Rhinanthus minor*, *Trixago apula*, *Melampyrum pratense*, *Euphrasia minima* (see figs. 299⁶ and 299⁷). In these plants we find, in general, a repetition of the entire process above described, except for the circumstance that the pollen is not adhesive but mealy, and is not transferred to the receptive tissue by appression of the stigma to the anthers—it being sufficient to place the stigma under the anthers by means of an inflection of the style. The stamens in this case are of the sugar-tongs type (cf. p. 271). In the first and second stages of floral development the mealy pollen only falls out of the anthers on the occasions when the stiff filaments of the stamens are forced apart by insects. Should no insects visit the flower the pollen remains in the loculi. In the third stage of flowering the filaments become flaccid, as does also the portion of the corolla adjacent to them, and in consequence the anthers, which have hitherto been closely coherent, move a little apart from one another and let the pollen fall out. Meanwhile the style has bent down sufficiently to bring the viscid stigma under the front pair of anthers, so that a portion of the pollen is caught upon its glistening surface, with the result that autogamy is effected (see fig. 299⁷). It is not uncommon for the inflection of the upper third of the style to be so strong as to amount to an involution, and the stigma is then pushed between the disuniting anthers and comes into contact with the hairs which clothe the anthers, and which are usually powdered all over with pollen.

Tricorytes, *Morina*, and the Rhinanthaceæ just mentioned, are all protogynous, whilst on the other hand, the Evening-primrose, Willow-herb, Campion, and Mallow, in which autogamy likewise occurs in consequence of the style bending down to the anthers, are protandrous. When the petals of the Evening-primrose (*Oenothera biennis*, *O. muricata*, &c.), or of the large-flowered species of Willow-herb (*Epilobium hirsutum*, *E. angustifolium*, see fig. 300) expand, the four branches of the style, which bear the receptive tissue and constitute the stigmas, are closely

coherent, whilst a further condition, which would also render pollination impossible, consists in a lateral inclination or sharp inflection of the style which removes the stigma out of the way leading to the honey. The eight anthers then stand in front of the spots where honey is to be obtained, and liberate their pollen in turn. A little later—half an hour in Evening-primroses, and 24 hours in the large-flowered species of Willow-herb—the style straightens itself and takes up a central position



Fig. 300.—Autogamy in the flowers of the Willow-herb (*Epilobium angustifolium*).

in the flower, whilst its four branches open back and present themselves in the form of a cross in front of the entrance to the honey. The stigmas remain in this position for a short time, and there is no need to enter into more detail to make it evident that cross-pollination may now be effected by the humble-bees which come in search of honey and bring with them a store of pollen from younger flowers. Soon afterwards, the four stigmas bend or roll back, bringing their receptive tissue into contact with the pollen still adhering to the anthers (see fig. 300, the lower flowers). This act of autogamy is usually promoted also by the stamens becoming rather more erect and by an inflection of the stalk-like inferior ovary in a gentle curve towards the ground, the result of which is that the flowers nod, *i.e.* are half-inverted.

Of the Ranunculaceae, a few species of Love-in-a-mist (*Nigella*) exhibit the same kind of contrivance. The flowers are protandrous. The first event to take place after the expansion of the sepals is a bending of the stamens in regular sequence towards the periphery of the flower, whereby the open anthers are posted just above the nectaries full of honey. Insects coming in search of honey must inevitably rub against the anthers in that position and dust themselves with the pollen. After the stamens have all accomplished these movements, the styles, which have hitherto stood stiffly erect and stationary, enter upon an active phase and bend outwards until their terminally-placed stigmatic tissue, which, meantime, has become mature, rests over the nectaries. In this position the stigmas are certain to

be dusted with pollen from younger flowers brought by the insects which come in search of honey. The process of outward inflection of the styles is, however, not yet completed, but continues until the stigmas strike against the anthers and take from them some of the pollen still clinging to their surfaces.

There are also some caryophyllaceous plants (*Lychnis alpina*, *Alsine Gerardi*, *Cerastium arvense*, *C. lanatum*, *Stellaria graminca*, *S. Holostea*) which exhibit, just before the flowers wither, inflections enabling the stigmas to possess themselves of the pollen of the anthers in the same flower. The flowers are incompletely protandrous. First of all, the stamens inserted opposite the sepals come to maturity while the stigmas in the same flower are still incapable of receiving pollen. The pollen offered by these stamens can therefore only be used for cross-fertilization. The next day their filaments bend as far as possible towards the periphery of the flower, and many of them lose their anthers. Meanwhile, the stamens standing opposite the petals grow longer and their anthers dehisce so that their pollen also is rendered available for transference by insects. A day later these stamens bend slightly towards the periphery of the flower, but they never lose their anthers, which continue to offer their pollen till the flower withers. On the fourth day the styles, which have hitherto stood in the middle of the flower, separate from one another, curve over backwards, and, in some species, become twisted into spirals. The stigmas are thus brought into contact with the anthers last mentioned and take up some of the pollen with which they are covered.

In the Caryophyllaceæ whose names are given above the inflections of stamens and styles take four or five days; in Mallows (*Malva borealis*, *M. rotundifolia*, &c.) the same processes are completed within 48 hours, and in *Hibiscus Trionum*, and in *Abutilon Arvense* within from three to eight hours. When the flower of a Mallow is just open a sheaf of filaments bearing round anthers covered with pollen may be seen enveloping and roofing over the styles. Soon after, however, the filaments of which the sheaf is composed become reflexed and a bundle of styles is then seen occupying the place previously filled by the stamens. The stigmatic tissue has matured in the meantime. The parts of the flower do not remain long in this position, which is obviously adapted to cross-fertilization by insect agency; the styles coil into the shape of an S and at the same time bend down until the fringe of papillæ constituting the stigmatic tissue comes into contact with the pollen of the anthers which have shortly before been lowered by the inflection of their filaments. In *Abutilon Arvense*, which grows abundantly in Hungary on the banks of the river Theiss, the sheaf of filaments does not at any time form a roof over the style, but, from the moment the petals unclose, five slender styles, terminating in spherical red stigmas with velvety surfaces, may be seen projecting above the anthers. Insects alighting upon the velvety stigmas or brushing against them may cause heterogamy at this period; but a couple of hours later the styles curve down, and the stigmas are appressed to the anthers which are covered with an abundant store of pollen. Other Malvaceæ, e.g. *Anoda hastata*, behave in an opposite manner as regards the inflection of the style. In the buds of these plants

both filaments and styles are sharply bent over towards the floral receptacle. After the expansion of the petals, the filaments straighten out and together constitute a sheaf of filiform stalks, each of which bears an anther covered with pollen. A little later it is the turn of the styles to become erect. They perform the same movements as have previously been executed by the stamens, and push themselves into the midst of the stamens. By these evolutions the stigmas of the longer styles are placed a little above the anthers, whilst those of the shorter styles are brought into direct contact with the anthers, and take from them some of the pollen of which there is always a certain quantity left so that autogamy invariably ensues.

The method of self-fertilization adopted by the Sun-dew (*Drosera*) is somewhat like that just described. In *Drosera* the spherical ovary supports three styles, each of which divides into two spatulate lobes bearing the stigmatic tissue on their upper surfaces. The open flower is cup-shaped, and in it these lobes may be seen spread out horizontally like the spokes of a wheel (see fig. 279¹⁰, p. 279). The stamens, on the other hand, are erect, and cross the lobes at right angles, holding the anthers above the stigmatic tissue. As soon as the petals begin to close, the stigmatic lobes rise up until they touch the anthers.

In several Labiates and Lentibulariaceæ autogamy is dependent on inflections, not of the style but of the stigma. This occurs, for instance, in the Hemp-Nettle (*Galeopsis ochroleuca*, *G. Tetrahit*, &c.), where the flowers are protandrous, and so adapted as to ensure cross-fertilization in the event of insects visiting them. Towards the end of the flower's period of bloom the stigmatic extremity of the lower arm of the style bends downwards and backwards until it touches the pollen-coated anthers of the longer stamens; in the case of many species of the Woundwort genus (*Stachys palustris*, *S. sylvatica*, &c.) both stigmatic arms bend down a short time before the flower fades and take the pollen from the anthers. The flowers of the Butterwort (*Pinguicula*; see vol. i. plate II. p. 142), which face sideways, contain two ascending stamens terminating in patelliform anthers, and above them an egg-shaped ovary surmounted by a large lobate sessile stigma. The lower border of the stigma which bears the receptive tissue hangs down like a curtain over the anthers. Insects, in the act of inserting their probosces into the honey-containing spur, brush first against this stigmatic border, and next against the anthers behind it. Thus they dust the stigma with the pollen they bring from other flowers, and the next moment load themselves with a fresh store which they carry off to yet other plants. The conditions are, in the first instance, adapted to cross-fertilization, and very frequently this form of reproduction occurs in the plants in question; but if no insects visit a flower the pendent stigmatic border rolls up sufficiently to bring the receptive tissue against the anthers. There being still plenty of pollen on the anthers, autogamy is then certain to ensue. The same phenomena may be observed in flowers of the Bladder-wort (*Utricularia*), and probably in those of the majority of Lentibulariaceæ.

A comparatively rare method of autogamy is for both filaments and style to coil up in spirals and become entangled just before the flower fades, the stigmas being

brought in the process of involution into contact with the pollen of one or more anthers. Most of the plants which exhibit this curious phenomenon have the common property of being ephemeral, but they belong to most different families. In a number of Commelynaceæ—*Commelyna cælestis*, for example (see fig. 301)—the stigma is situated in front of and lower than the anthers when the flower, which faces sideways, is quite newly open (fig. 301¹). Honey is secreted on curious palmately-lobed nectaries, and if in this first period of the flower's development insects come in quest of the honey they make use of the anthers to alight on, and in so doing besmear themselves with the pollen, which is already emerging through the lateral sutures of dehiscence of the anthers. Soon afterwards the stamens become spirally coiled, and the style, which meanwhile has grown to the same length as the stamens, curves in such a manner as to bring the stigma to a somewhat higher position than it previously occupied, and to make it the most con-



Fig. 301.—Autogamy by means of spiral twistings of stamens and style.

¹ Flower of *Commelyna cælestis* in its first stage. ² In its second stage. ³ In its third stage of development. All in longitudinal section and slightly magnified.

venient place for insects to settle upon (fig. 301²). The arrival of insects which have visited younger flowers is at this stage sure to be accompanied by cross-fertilization. This state of affairs, however, only lasts a very short time. The style then winds itself into a spiral, and becomes entangled with the coiled stamens, with the inevitable result that the stigma comes into contact with one or other of the anthers, and gets covered with pollen (fig. 301³). The whole process occurs in almost exactly the same manner in the flowers of *Allionia violacea*, of *Mirabilis Jalapa*, and several other Nyctaginaceæ. As regards *Allionia violacea*, it is only necessary to observe that the flowers are protogynous, that the stigma is higher than the anthers at 6 a.m., when the flower opens, that a few hours later the anthers are raised to a higher level than the stigma in consequence of certain peculiar movements of the style and stamens, and that by 10 o'clock the involution of the filaments resulting in autogamy has already begun. In the newly-opened flower of the Marvel of Peru (*Mirabilis Jalapa*) the dot-like stigma is situated in front of the anthers, and in the event of insects coming in search of honey, it is first the papillæ of the stigma and afterwards the anthers that are touched by the intruders. No raising and lowering of filaments or style takes place in this case,

but a process of involution like that exhibited in *Allionia* ensues, and as soon as autogamy has been initiated the limb of the perianth folds up, turns pulpy, and then forms a kind of stopper above the knot of twisted filaments and style. The flowers of the Purslane (*Portulaca oleracea*) differ from those of *Commelyna*, *Allionia*, and *Mirabilis* in having five stigmas which are like delicate feathers in form, and are spread out in a star in the middle of the erect flower-cup. The stamens project obliquely from the receptacle, and are arranged in a circle round the stigma; but when the flower opens first, there are little spaces between anthers and stigmas, and this prevents a spontaneous transference of pollen to the stigmas. After the lapse of a few hours the petals, which in the sunshine are expanded in the form of a cup, draw together, and the flower begins to close up; all the five feathery stigmas bend over to the same side and gradually coil up into spirals. The thread-like stamens also undergo inflection, at first into semicircles, and subsequently into spirals, and the pollen-coated anthers are in consequence pressed against the stigmas. At this period, in the Purslane as in the Marvel of Peru and other plants whose flowers are ephemeral, the petals may be seen in a pulpy condition covering over the knot of tangled filaments.

As has been said before, this form of autogamy occurs chiefly in flowers which last only a single day. Where the whole period during which the flower is open is but a few hours the movements in question may all be followed by the observer. In the few species, which resemble the foregoing in respect of autogamy, but differ from them in that their flowers remain open two or three days, or even longer, these movements of inflection and torsion take place much more slowly. Thrifts (*Armeria alpina*, *A. vulgaris*, &c.) display in the middle of each of their cup-shaped flowers five stigmas disposed in the same manner as those of Purslane-flowers. The stigmas in this case, however, are not feathery, but in the form of slender cylinders covered with short, closely-packed papillae, which give them a velvety appearance. The stamens are adnate to the short corolla-tube, and rise up in front of the petals holding their anthers between the rays of the stigma. Notwithstanding the proximity of the anthers to the stigmas, neither in the first nor in the second stage of the flower's development is any pollen transferred, without extraneous aid, to the receptive stigmatic tissue. At first the stamens are so placed as to have their anthers brushed by insects visiting the flower, whilst the five stigmas are still erect. A little later the anthers and stigmas change places as in so many other cases; the stamens stand up and bring the anthers together nearer the middle of the flower, whilst the stigmas diverge from one another, and place themselves close to the way leading to the honey. Attention has been so often directed to the connection between an interchange of position of this kind and the accomplishment of cross-fertilization that it is needless to repeat the facts of the case. Supposing, however, that insects do not visit the flower, and that, in consequence, heterogamy fails, the styles wind themselves up spirally, and move at the same time towards the middle of the flower, where they become entangled with the filaments, which have likewise undergone spiral torsion. In these circum-

stances, the velvety stigmas cannot fail to receive the pollen that still adheres to the anthers.

It appears from what has been said concerning autogamy that in a large number of plants the pollen developed in the anthers, especially if it be of the adhesive variety, still occupies the recesses of the anthers, or sticks to the reflexed margins of the lobes after their dehiscence, at the time when the flower fades. Even after insects have brushed off a portion of the pollen and transported it to other flowers, there is still invariably an abundant supply for the purpose of autogamy, and it is only in rare cases that loculi, in which adhesive pollen has been matured, are completely emptied by the end of the flowering period. In some plants, however, the adhesive pollen is swept out or removed in some other way from the anthers by means of special contrivances as soon as it is mature, and is then deposited on some particular spot in the flower where it is exposed for dispersal. In the case of the pollen of Composites it is well-known that it is pushed out of the tube of connate anthers by the style, owing to the growth of the latter organ which is sheathed within the anther-tube, and that it appears at the top of the tube in the form of a lump capping the extremity of the style. In Bell-flowers (*Campanula*), the entire contents of the anthers are stored upon the surface of the style, and the same thing happens in the various species of the Rampion genus (*Phyteuma*) and in some small-flowered Gentians. The shrivelling of the anthers is in many plants the cause of their shedding a portion of their pollen, and it may then collect on capillary appendages of the ovary, in cup-shaped petals, or on some other part of the flower where it is stored up for future use. It must often happen, too, that when insects are in the act of taking the honey they push against the stamens, and that the pollen shaken out of the anthers by their impact adheres to particular parts of the corolla, calyx, or perianth. This pollen is just as available for fertilizing purposes as that which remains sticking to the anthers, and we meet with cases where the stigmas fetch the pollen developed in the same flower from its temporary resting-place, and so bring about autogamy. Contrivances for this purpose are not numerous, but the number of species in which this form of autogamy prevails is extremely large. The abstraction of pollen deposited on the outer surface of the stylar column or its arms by stigmatic tissue situated on the edges or the inner surface of these style-branches occurs in hundreds of Campanulas and thousands of Composites, and shall therefore be chosen as our first example of this type of process.

Two modes of operation may be distinguished: first, a crossing; and, secondly, a spiral revolution of the style-branches. The former process is observed particularly in the Asteroideæ (*Aster*, *Bellidiastrum*, *Erigeron*, *Solidago*), especially in the tubular flowers in the middle of the capitula of these plants; but it is also seen in many Composites possessing ligulate flowers only. In *Aster alpinus*, the species selected for illustration (see figs. 302^{1, 2, 3}), the stylar arms are short and thickish; their inner surfaces are smooth and flat, whilst their outer surfaces are a little arched, and towards the free extremities are furnished with papilla-like sweeping-hairs. The receptive stigmatic tissue is situated on the margins of the style-

branches below the sweeping-hairs, and may be recognized by the granulated appearance of its turgescient cells. The behaviour of the styler branches from the commencement to the termination of a flower's bloom is shown in fig. 302¹, where the three tubular florets are in successive stages of development. Almost simultaneously with the opening of the tubular corolla the two style-branches are pushed up above the anther-tube, and the pollen is swept out of the tube by the hairs previously referred to. The style-branches at this period are in close contact, and the receptive tissue of the stignas is not yet accessible (fig. 302¹, left-hand floret).



Fig. 302.—Autogamy by means of a crossing or a bending back of the style-branches.

¹ *Aster alpinus*. Portion of a capitulum, including a marginal female floret with ligulate corolla and three tubular florets of the disc. The latter are in the successive stages which lead to autogamy (left to right). ² Style-branches of *Aster alpinus* which have just separated but still have some pollen clinging to their hairs. ³ The style-branches crossed so as to transfer the pollen from the collecting-hairs of the one to the stigmatic tissue of the other. ^{4, 5, 6} Florets from the centre of a capitulum of *Centaurea montana* in successive stages leading to autogamy. ⁷ The two style-branches rolled back sufficiently to bring the stigmatic tissue into contact with the pollen on the collecting-hairs. ⁸ *Campanula persicifolia*; longitudinal section through a newly-opened flower. ⁹ The same with the style-branches rolled back so as to bring the stigmatic tissue into contact with the pollen on the exterior surface of the stylar column. ¹⁰ Flower of *Phyteuma orbiculare* in process of transition from the first to the second stage of development. ¹¹ The same flower in the last stage of development. ^{8, 9} natural size; the rest magnified.

Neither cross- nor self-fertilization of the flower in question can at present be effected, and the pollen is only exposed that it may be carried away by insects to fertilize other blossoms. The two style-branches are subsequently lifted still higher and move a little apart, with the result that the pollen clinging to their hairs, if not already removed by insects, is for the most part pushed off, falls down, and is appropriated to the purpose of geitonogamy (see p. 321). A small remnant of pollen is, however, invariably left hanging to the lower collecting-hairs, and this it

is which is devoted to autogamy (see fig. 302²). The process of self-pollination is the last to take place. The two style-branches bend and cross one another, and in so doing bring the pollen adhering to the lower hairs of the one arm into immediate contact with the receptive tissue on the margin of the other arm. In this position the two style-branches resemble the beak of a cross-bill, as may be seen in fig. 302³. The style-branches of those Composites whose capitula consist entirely of ligulate florets, are always much longer than those of the Asteroideæ; they are of thread-like appearance, and the lower parts of their external surfaces are beset with collecting-hairs. In one section of these Composites, including, for instance, *Crepis grandiflora*, *Hieracium umbellatum*, and *Leontodon hastile*, there is likewise, shortly before the flowers fade, a simultaneous inflection and spiral involution of the two branches of the style resulting in autogamy; it reminds one, even more forcibly than the case of Asteroideæ, of the action of a person when he crosses his arms.

The second kind of process, viz. the spiral re-volution or bending back of the style-branches, may be particularly well seen in the Groundsels—*Senecio Fuchsii* and *S. nemorensis*—and in Centaureas. We will select as an example *Centaurea montana* (see figs. 302^{4, 5, 6, 7}), which grows abundantly in the lower Alps. The styles are fashioned quite differently from those of the composite flowers to which reference has been made above. The stigmatic tissue is spread out over the inner surface of the style-branches, especially over the part near the free extremity, and the collecting-hairs are confined to a narrow zone underneath the point of bifurcation of the style. The pollen is swept out of the anther-tube (see fig. 302⁴) in the same manner as in the other Composites, but in *Centaurea* the process of extrusion is accelerated by a sudden contraction of the irritable filaments of the stamens when they are touched by insects (*cf.* p. 252). After most of the extruded pollen has been removed by insects or scattered by the divergence of the style-branches (fig. 302⁵), the receptive inner faces of the latter are so disposed as to ensure cross-pollination in the event of insects coming laden with pollen from other capitula. This state of affairs, however, only lasts a short time; the two style-branches soon roll back and bring the receptive tissue of their originally inner faces into contact with the pollen left upon the hairs, thus effecting autogamy (see figs. 302⁶ and 302⁷).

Bell-flowers (*Campanula*) exhibit for the most part the same bending back of the style-branches, and the phenomenon has the same significance in them as in composite flowers, but the manner in which the pollen is transferred to the external surface of the style is somewhat different. Within the closed bud the long anthers are adjacent to the central column of the style, as in Compositæ, and form a kind of tube round it. These anthers open inwards, too, and deposit the whole of their pollen on the outside of the style, which is furnished with delicate transparent papillæ, and is in consequence well adapted to the retention of the pollen. The pollen is not, however, swept out of the tube of anthers, but the anthers, after depositing their pollen upon the stylar column, separate from one another and shrivel up, and only persist as shrunk and empty relics at the bottom of the flower (see fig. 302¹). The style-branches are by this time divergent, and occupy a posi-

tion in the mouth of the corolla, which necessitates contact between the receptive tissue at their tips and the bodies of the humble or hive bees, which find their way to the flower in search of honey. If these insect-visitors bring with them pollen from other flowers, cross-fertilization is inevitable. As they push lower down into the flower, the bees receive an additional load of pollen from the stylar column, the surface of which is coated with it, and this new store they may convey to other blossoms. When the time for the flower to fade is near at hand, the style-arms become revolute, and press the receptive tissue of their tips upon the stylar column, taking from it a coating of pollen, of which there is still a sufficient quantity clinging to the surface (see fig. 302⁹). The large-flowered *Campanula persicifolia* has been selected as a type of these Bell-flowers. The style-arms in this species are from 1 cm. to 1.6 cm. long, and they coil into spirals of from $1\frac{1}{2}$ to 2 involutions. In most of the other Bell-flowers (e.g. *C. barbata*, *C. carpatica*, *C. pyramidalis*, *C. Rapunculus*, *C. spicata*) the revolute style-branches have only from 1 to $1\frac{1}{2}$ coils in each spiral, whilst in some few (e.g. *C. patula*, *C. rapunculoides*) there are rather more than 2 complete coils in each. The Rampion genus (*Phyteuma*), here exemplified by *Phyteuma orbiculare* (see figs. 302¹⁰ and 302¹¹), differs from the Bell-flowers, which are its nearest allies, in the circumstance that the deposition of pollen and retraction of the emptied anthers occurs at a time when the tips of the petals are still connate into a tube. For a short time the end of the stylar column may be seen covered with pollen projecting beyond the corolla, and in this position the two arms disunite and expose their stigmatic tips to pollination by insects (see fig. 302¹⁰). If no insects visit the flower the style-branches roll back and bring their tips into contact with the pollen on the stylar column (see fig. 302¹¹). In all the species that have been examined (*Phyteuma confusum*, *P. hemisphaericum*, *P. Halleri*, *P. orbiculare*, *P. spicatum*) the style-branches are wound into from 1 to 2 complete coils. In the case of *Phyteuma Halleri* the further observation was made, that after the accomplishment of autogamy the transparent hairs on the stylar column and the pollen adherent to them rapidly dry up, whilst the branches of the style unroll again.

Of the Gentians, the little *Gentiana prostrata*, which grows on the mountains in the vicinity of the Brenner Pass in Tyrol, affords a striking example of the phenomenon in question. The flowers are protandrous: the anthers in the bud are contiguous to the short style and closed stigma, and, when they open, their pollen is deposited upon those organs. Upon the expansion of the corolla, the pollen is available for other flowers through the agency of insects. Somewhat later the stigmatic lobes part, and if after this insects visit the flower, they brush against the receptive spots of the stigma, and may dust them with extraneous pollen. Lastly, the two stigmatic lobes curl back until the receptive tissue upon their upper surfaces reaches the residue of pollen still sticking to the short style.

Much less common modes of operation are for the revolute stigmas to take the pollen from the edge of the tube of connate anthers, from hairs on the corolla, from bristles on the pappus, or from depressions in the petals. The case of abstraction

of pollen by stigmas from the edge of the anther-tube I observed in several Composites, as, for instance, in the species of the genera *Adenostyles* and *Cacalia*, and in *Arnica montana*. The external surface of the style in *Adenostyles* is beset with papillae, which give it the rough glandular appearance whence it derives its name of *Adenostyles* (= glandular style): it has no collecting-hairs, and the pollen is therefore not swept but squeezed out of the anther-tube. The edge of the tube is furnished with prongs, each of which is slightly revolute and is concave almost to the extent of being boat-shaped, so that it is able to retain some of the extruded pollen. This pollen is only used for autogamy in the event of the stigmas not being dusted in any other way. In that case the two style-branches roll back until the receptive

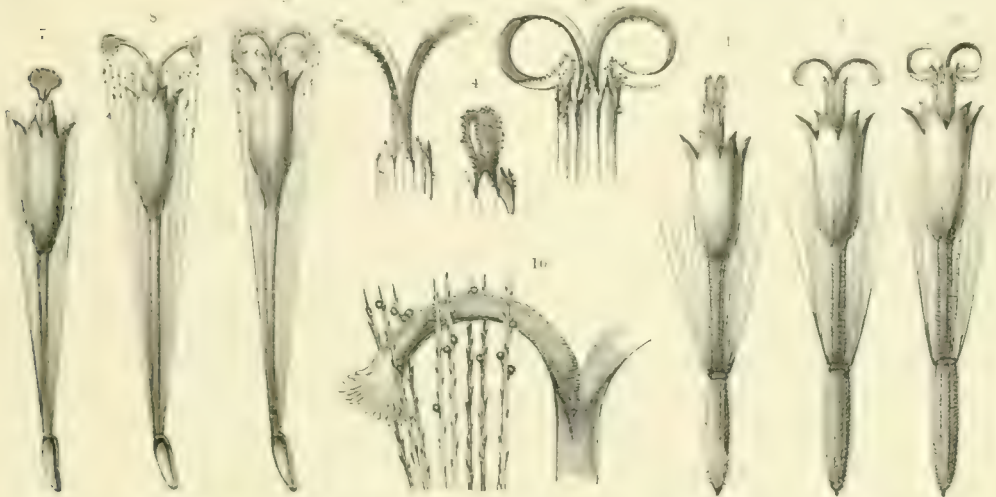


Fig. 303.—Autogamy effected by means of an inflection of the style-branches.

1, 2, 3 Flowers of *Arnica montana* in successive stages leading to autogamy. 4 Style-branches of *Arnica* in contact shortly after their extrusion from the anther-tube. Pollen is clinging to the collecting-hairs and to the mouth of the tube. 5 The style-branches projecting still further from the tube and diverging from one another. 6 The style-branches curved back so as to bring the stigmatic tissue into contact with the pollen sticking to the tube of anthers. 7, 8, 9 Flowers of *Senecio viscosus* in the successive stages of development leading to autogamy. 10 A revolute style-branch of *Senecio viscosus* with its stigmatic tissue in contact with the pollen sticking to the bristles of the pappus. All the figures magnified.

tissue comes into contact with the edge of the anther-tube. The style-branches in *Arnica montana* (see figs. 303^{1, 2, 3, 4, 5, 6}) have collecting-hairs on the surface of their slightly-thickened tips only, and in this case the pollen is regularly swept out (figs. 303¹ and 303⁴). A small quantity of the pollen is always left behind upon the 5-toothed edge of the anther-tube. The manner in which the pollen is transferred to the stigmatic tissue by means of the re-volution of the style-arms is shown in the accompanying figure 303⁶.

As illustrations of the abstraction of pollen from the hairs of the corolla we may take a campanulate, a labiate, and two caryophyllaceous species. The corolla of the Nettle-leaved Bell-flower (*Campanula Trachelium*) has a thick coating of hairs on its inner surface. In the bud these hairs are directed horizontally towards the axis, and touch the style and the anthers. The deposition of the pollen upon the stylar column takes place in the same way as it does in the Bell-flowers already

discussed (see p. 361), but the moment the anthers are retracted some pollen is invariably caught by the hairs of the corolla, and when the flower opens a portion of the pollen is always to be seen adhering to them. The humble and hive bees which visit the flower may, of course, bring about cross-fertilization, just as they do in the other Bell-flowers. The style-branches in *Campanula Trachelium* do not, at the close of the flowering period, roll back so far as the central column; a less degree of bending is here adequate to bring the receptive tissue on the tips of the style into contact with the pollen sticking to the hairs.

In *Dianthus neglectus*, a species of Pink indigenous to the Southern Alps, and in the Glacier Pink (*Dianthus glacialis*), the laminae of the petals are beset with hairs. The pollen is first exposed to the chance of dispersal by insects, but afterwards the stamens curve outwards, and some of the pollen becomes affixed to the hairs of the petals, which usually receive in addition a small deposit as a result of the scattering action of insect-visitors. The flowers are protandrous. The stigmas, which are situated in front of the entrance to the floral interior, wait till the period of the flower's bloom is nearly at an end, for the chance of being touched by insects bearing extraneous pollen. But sometimes no insects come, and in that case the pollen stored upon the hairy laminae of the petals is made use of at the last moment. The transparent papillose stigmas wind themselves into the shape of the letter S, and, sweeping like a brush over the petals, collect the pollen from them. This operation is materially assisted in both the Pinks under discussion by the fact that the laminae of the petals grow some millimetres longer during the flowering period, the result of which is to bring the hairs besmeared with pollen a little nearer to the stigmas. In *Dianthus neglectus* there is besides an involution and uprising of the laminae in the evening, which, likewise, assist the process of sweeping up the pollen by the stigmas.

In *Ballota nigra*, a Labiate with protandrous flowers which grows commonly in hedges on cultivated land, some of the pollen falls at the very commencement of the flower's bloom upon the hairs clothing the borders of the upper lip. If no pollen is brought by insects to the stigma of a flower of this plant, the lower style-arm bends down at the end of the flowering period and takes up the pollen from the hairy mantle above referred to. The same kind of thing happens in a few other Labiates, as, for instance, in *Salvia viridis*, of the Mediterranean flora, whose style bends down in the event of a failure of insects, and brings the stigma into contact with a store of pollen resting upon the under-lip, where it fell at the very commencement of the flower's bloom. I have hitherto observed only in the cases of *Tozzia alpina* and *Pyrola media* the phenomenon of a style curving down to take pollen from cup-shaped hollows in the corolla in which it has lain stored, but it probably occurs in many other plants besides.

The curious case of the pollen being taken from the hairs of the so-called pappus by the stigma is illustrated in figs. 303^{7, 8, 9, 10}. In the Stinking Groundsel (*Senecio viscosus*), which will serve for an example, the style-branches are furnished at the tips only with bunches of collecting-hairs. As the style elongates these hairs sweep

the pollen out of the tube of anthers and leave it in a round lump at the top of the tube (see fig. 303⁷), whence it may be carried off by insects. At this stage the corolla and the hairs of the pappus are 6 mm. long. Soon afterwards the two style-branches, which have undergone rapid elongation, part asunder, and the pollen, if not already removed by insects, is shaken off, and falls on to the pappus-hairs, where it is caught by the asperities on their surfaces (see fig. 303⁸). The receptive tissue on the inner faces of the style-branches, which are now the upper surfaces, are in a position to get dusted with pollen brought by insects from other flowers. Meanwhile an elongation of every part of the flower has taken place; the pappus-hairs have attained a length of 7 mm., and the corolla of 6.5 mm. Lastly, the flower enters upon its third stage of development. The two style-branches curve down, bringing the stigmatic tissue into contact with the pollen sticking to the pappus-hairs, which have by that time grown another millimetre, and are therefore reached all the more easily, as they even project above the arms of the style (see figs. 303⁹ and 303¹⁰).

In all the cases hitherto dealt with the only parts of the flower which are concerned in bringing about autogamy are the stamens and pistils. The filaments in some instances, the parts bearing stigmatic tissue in others, undergo inclination or inflection, whilst sometimes both organs mutually approach one another. No direct part in the process of autogamy is taken in any of these plants by the whorls of petals surrounding the stamens. We will now proceed to describe cases in which the petals are instrumental in effecting self-fertilization.

The simplest case of the discharge of this function by *petals* is to be found in flowers which are in the shape of tubes, cups, or basins, and whose anthers are adnate to the inner surfaces of the petals, and are brought into contact with the stigma in consequence of a contraction or closing together of the corolla—*Thymelaea Passerina*, a low shrub belonging to the Thymelaceæ, will serve as an example. The small inconspicuous flowers of this species contain nectar, and by its perfume attract insects which brush pollen from the anthers as they suck the honey and convey it to the stigmas of other flowers. The anthers are adnate to the inner face of the cup-shaped perianth, and are at first at a distance of only $\frac{1}{2}$ mm. from the stigmas. Notwithstanding this proximity the viscid pollen is not spontaneously transferred to the adjacent stigma when the flower is first open. It is not till the flower is nearly over that a slight contraction of the upper third of the perianth causes the anthers to be pressed against the stigma, which stands at the same level as themselves. In *Claytonia perfoliata*, one of the Portulacæ, autogamy is effected in the same manner, the only difference being that the anthers are borne on special filiform filaments which are adnate to the bases of the petals. These filaments, however, share in all the petals' movements, and the anthers at their extremities are pressed exactly upon the stigma when the corolla closes up.

In other cases the epipetalous stamens hold their anthers at the commencement of the flowering period underneath or behind the stigmas, and are pushed upwards during the flowering period by an elongation of the petals, in consequence of which

they rest in the last stage against the lateral edges of the stigmas. This process is very common in plants of the order Solanaceæ (*Hyoscyamus*, *Lycium*, *Nicotiana*, *Physalis*, *Scopolia*), and it has also been observed in Gentianaceæ (e.g. *Erythra pulchella*, *Gentiana campestris*, *G. glacialis*). In some of these plants the elongation undergone by the corolla-tube is very considerable as compared with the size of the flower. In the American Tobacco plant (*Nicotiana Tabacum*) it amounts to nearly $\frac{1}{2}$ cm., whilst in the little Centaury (*Erythraea*) it is only 2 mm. The elongation of the corolla-tube is accompanied in most instances by a stretching of the filaments. In consequence of this combined growth the anthers are, in the case of the short-styled flowers of *Lycium barbarum*, raised $\frac{1}{2}$ cm. in 24 hours. In the Henbane (*Hyoscyamus niger*) the anthers are 7 mm. lower than the stigma in the morning when the flower is nearly open, but by the evening of the same day the simultaneous elongation of the corolla-tube and of the stamens adnate to it has raised the anthers to the level of the stigma and pressed them upon it. It is scarcely necessary to mention that in these plants, which are all protogynous, cross-fertilization is possible in the first part of the flowering period, and it is as a matter of fact very frequently effected through the intervention of insects.

A very curious variety of the phenomenon in question is exhibited by the large-flowered species of the Eyebright genus (*Euphrasia Rostkoviana*, *E. versicolor*, *E. speciosa*), and by the allied Yellow Rattles (*Rhinanthus angustifolius* and *R. hirsutus*). The flowers of these plants face sideways, and the corolla has a tri-lobed under lip and a bi-lobed helmet-shaped upper lip. Four stamens of the pollen-sprinkling type, which we have compared to sugar-tongs, are adnate to the corolla-tube. The anthers are concealed beneath the upper lip; the long filiform style is in the shape of the letter S and lies above the anthers, and when the flower is first open it projects considerably beyond them (see fig. 277⁴, p. 273). Stigma and anthers are then so placed as to make it inevitable that insects which enter the flower shall first touch the stigma, and the next moment become dusted with a shower of pollen from the anthers. If several blossoms are visited in succession cross-fertilization is certain to take place. If, however, insects stop away, the tube of the corolla elongates and carries up with it the epipetalous stamens. As the style retains its original length, the terminal stigma, which hitherto has projected in front of the anthers, now rests by the side of the anthers or just above them. Thus the stigma is in a sense overtaken by the anthers. In the large-flowered species of Eyebright the tense style then presses upon the anthers, forces them asunder, and, sinking down, brings its stigma between the anther-valves, where it cannot fail to get coated with the pollen of which they are still full. In the species of Yellow Rattle above mentioned, the stamens become flaccid towards the end of the flower's period of bloom and the pollen falls out and is left sticking to the hairs of the anthers or to the involute folds of the corolla, so that the style in brushing by usually removes it.

It is much less common for the calyx to play this part in bringing about autogamy. *Tellima grandiflora*, a North American Saxifragacea, is the only case

known at present in which the stigma after being at first rather higher than the anthers is overtaken by them and besmeared with pollen owing to an elongation of the calyx and consequent raising of the stamens, which are adnate to the tube of the calyx.

In many plants autogamy depends upon the fact that as the corolla falls off, its tube slips over the stigma, so that the latter rubs against the anthers, which are still laden with pollen, or against the inside of the corolla, which is also besmeared with that substance. This process presupposes that when the flower is in full bloom the anthers are overtopped by the stigma, and that the latter is still in a receptive condition at the time the corolla becomes detached and drops. Both these conditions are as a fact fulfilled in all plants of this category. In the species of the genus *Gilia* (Polemoniaceæ), and in the Brazilian plant *Psychotria leucocephala* (Rubiaceæ), the long filiform styles branch into divergent arms, which bear the delicate stigmatic tissue; and at the period of full bloom, these style-arms project far above both the limb of the corolla and the anthers. Consequently, insects alighting on these flowers encounter first of all the stigmas, and if they are laden with foreign pollen they occasion cross-fertilization. There is, on the other hand, in this form and position of the stigmas the further advantage, that, in case of a dearth of insect-visitors, the stigma may still acquire a supply of pollen when the corolla falls off—that is, at the very last moment of flowering. It is not unusual in these plants to see the corolla, after it has become detached, hanging for quite a long time from the long style and divergent stigmas, and this delay in the process of severance must materially assist the accomplishment of autogamy. The detached corolla persists in a similar manner in flowers with capitate, or short-lobed stigmas, as, for instance, in *Rhododendron hirsutum*, in *Digitalis*, *Achusa*, *Cestrum*, and various other Scrophulariaceæ, Boraginaceæ, and Solanaceæ. In the case of *Rhododendron hirsutum*, as the corolla slips along the style, the stigma brushes off the pollen, which has invariably been discharged from the anthers before the flower opens and been caught upon the hairs in the interior of the corolla-tube. In *Cestrum aurantiacum*, the anthers, which are borne upon stiff and slightly-inflexed filaments, are pressed against the style, and the corolla is left hanging from the style, usually for a couple of days after its detachment, and does not fall till after fertilization has taken place, when the style also drops off. A great variety of contrivances exists with the object of promoting this method of autogamy by means of a falling corolla. A brief account of three of them will now be given. The flower of the Moth Mullein (*Verbascum Blattaria*), which may be taken as the type of a large number of flowers of Scrophulariaceæ, has a corolla with a very short tube and the limb spread out at right angles to it (*rotate*). Adnate to the tube are five stamens clothed with woolly hairs of a violet colour. The three upper stamens are a little shorter than the two lower ones, and all of them project obliquely beyond the limb of the corolla. The central style is still further exserted, and serves as a perch for insects to alight upon. It is obvious that so long as the parts of the flower are disposed in this manner every insect which arrives with a supply of

pollen must effect cross-pollination. As in so many other cases, autogamy is reserved for the last moment of bloom. With a view to its ultimate achievement, the two longer filaments cross themselves over the mouth of the corolla-tube in somewhat the same attitude as a pair of folded arms. This brings their two anthers, which are still full of the orange-coloured pollen, behind the stigma. The corolla now becomes detached from the receptacle and falls forward, but remains for a short time suspended to the long style, where it undergoes slight torsion. Finally, it drops with a gyratory motion, and as it does so the stigma must inevitably be brushed by one or other of the anthers lying in front of the mouth of the flower. The Pimpernel (*Antyphalis*), which belongs to the order Primulaceæ, has a corolla resembling that of the Moth Mullein in being rotate and in containing five stamens clothed with violet hairs. The stamens in this case are very long, and the style is bent to one side, and passes between two of the stamens. Thus the stigma is out of reach of the anthers, and cannot, in the first stage of the flower's development, be dusted with their pollen. On the other hand, cross-fertilization may be effected by the small insects which creep over the flat limb of the corolla in order to feed on the hairs of the stamens. The flowers of the Pimpernel belong to the category of those in which the corolla opens and shuts periodically. The operation of closing is due to the expanded limb being thrown into superincumbent folds. On the second occasion of the flower's closing, the anthers come into contact with the part of the corolla that is folded in, and leave some of their pollen sticking to it. This pollen is still to be seen adhering to the inner face of the corolla on the following day, when the limb expands again, and there it remains till the evening, when the corolla closes for the third time. After this the corolla does not open any more, but falls off still closed, and, as it does so, brushes the style, which is held between two stamens, and leaves upon the stigma the pollen that was sticking to its inner surface. Again, there is the case of *Soldanella alpina*, to which we have already several times had occasion to refer in other connections, and also as affording an instance of a second form of autogamy (p. 333) besides that now in question. The style stands up in the form of a column in the middle of the bell-shaped corolla, and has the five stamens close to it. The anthers are united into a cone, and act as sprinklers in the dispersion of their pollen. When an insect pushes into a flower it rubs first against the stigma, and dusts it with foreign pollen, and as it forces its way further in it displaces the various parts composing the cone of anthers, and is consequently besprinkled with pollen. If no insects visit the flower the anthers are still full of pollen when the time comes for the corolla to drop off, and as the style is drawn through the dislocated cone of anthers, the pollen in the interior of the latter is caught up by the stigma, and self-fertilization is effected.

Next to these plants, in which autogamy takes place on the fall of the corolla owing to its tube slipping over the stigma, there comes a group of species in which the same result is attained in the following manner. At the time when the flower opens, the petals are slightly smeared with pollen, and this deposit forms a reserve store. Should the stigma not have received any pollen from extraneous sources, the

flower being nearly over, certain movements are undergone by the petals which result in the transference of the pollen sticking to their surfaces, margins, lobes, or folds, as the case may be, to it. The instances of this mode of effecting autogamy are very numerous, and it will be best to class them in small sub-groups, and to take a well-known example from each as an illustration.

In *Argemone*, *Hypecoum*, and *Specularia*, which will serve as types of the first group, there is no considerable elongation of the pollen-flecked petals during the

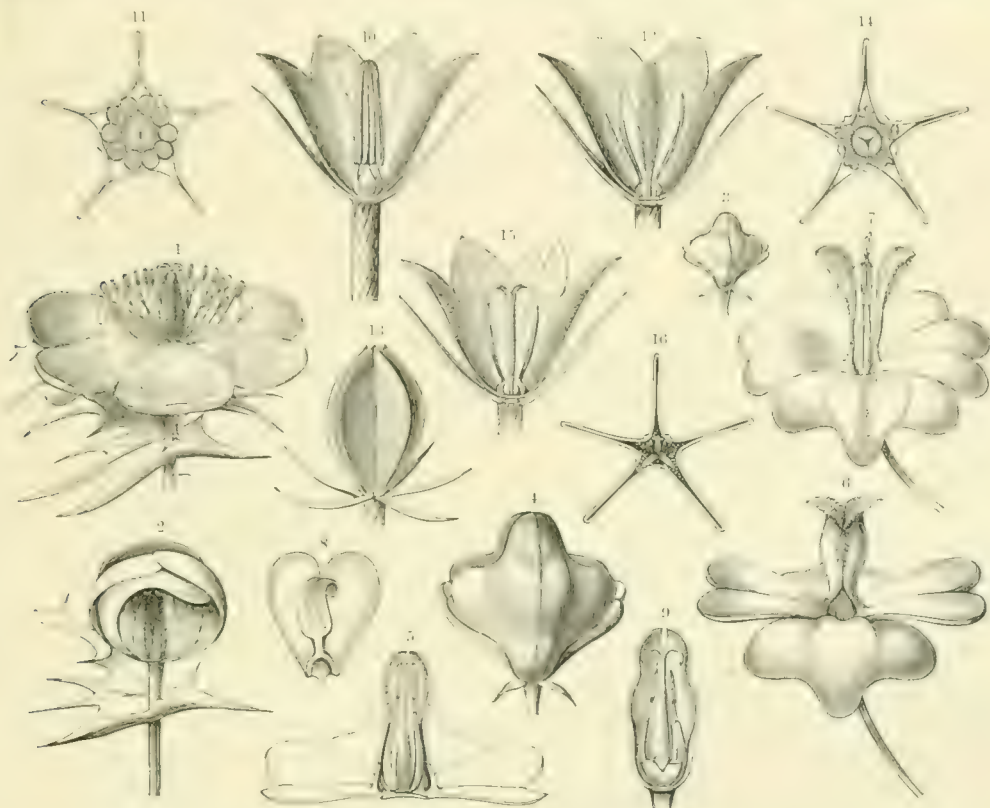


Fig. 304.—Autogamy effected by the petals.

¹ Flower of *Argemone Mexicana* open in the sunshine. Pollen which has fallen from the anthers is resting upon the concave petals. ² The same flower closed; one of the petals besmeared with pollen is laid upon the stigma; the front petal is removed. ³ Closed flower of *Hypecoum grandiflorum*, natural size. ⁴ The same magnified. ⁵ Longitudinal section through the open flower in the first stage of development. ⁶ Open flower in which the pollen-laden lobes of the inner petals are beginning to separate. ⁷ The same flower at a later stage. ⁸ One of the two inner petals; the middle lobe is coated with pollen; at its base is the pit containing the honey. ⁹ Longitudinal section through a closed flower in its last stage of development. ¹⁰ *Specularia speculum*; longitudinal section through an open flower in the first stage. ¹¹ Transverse section through a closed flower in the first stage. ¹² Longitudinal section through an open flower in the second stage. ¹³ Closed flower. ¹⁴ Transverse section through a closed flower in the second stage. ¹⁵ Longitudinal section through an open flower in the last stage. ¹⁶ Transverse section through a closed flower in the last stage. ^{1, 2, 3} natural size; the rest magnified.

period of the flower's bloom. This period is only a single day in the case of *Argemone*, and the process takes place in a very simple manner. In the morning, as soon as the petals are wide open and the tension of the sheaf of stamens surrounding the pistil is somewhat relaxed, there is an immediate fall of pollen on to the concave surfaces of the petals (see fig. 304¹). The flowers are erect, as also is

the pistil, and the stellate stigma, which offers the best alighting place for insects, rests at a slightly higher level than the anthers, and at a sufficient horizontal distance from them to prevent their pollen from reaching, spontaneously, its receptive tissue. In the course of the day insects arrive with pollen from other blossoms and cause cross-pollination. When the evening comes the petals close up over the pistil, and one of them brings its inner surface, which is covered with pollen, into direct contact with the stigma (see fig. 304²).

The case of the *Hypocoum* is far more complicated. The flowers of this plant have two small sepals and four large tri-lobed petals (see figs. 304³ and 304⁴). The latter are arranged in two pairs at right angles to one another, one pair being inserted a little higher than the other. The middle lobe of each of the petals belonging to the upper pair is curiously modified: its surface is concave, and in the young flower has the shape of a spoon with fringed edges. The function of these lobes is to collect all the pollen from the anthers at the very commencement of flowering. The anthers are, like those of *Compositæ*, coherent into a tube inclosing the style; but instead of opening inwards as the latter do, they are extrorse, *i.e.* dehiscence outwards. At the time of dehiscence and of the discharge of the pollen the two spoon- or pouch-shaped central lobes of the upper petals are in close proximity to the anthers, and they receive the whole of the pollen (see fig. 304⁵). After this transfer has been accomplished the two lobes now containing the pollen separate from one another, the first parts to disunite being the free extremities at the top, then the lateral edges (see fig. 304⁶). The pollen is thus exposed and may be carried off by insects which come for the honey concealed in a little depression at the base of each lobe (fig. 304⁸). The two linear stigmas being in close contact at this stage, their tissue is not as yet accessible; they do not disunite till two days after the first opening of the flower, but when that interval has elapsed they diverge, and then constitute the most convenient place for insects to settle upon. They are now in exactly the same position as was previously occupied by the pollen-laden lobes (see fig. 304⁷), and therefore if an insect alights upon them after visiting younger flowers, it is sure to dust the stigmatic tissue with foreign pollen. Meantime the petal-lobes which received the pollen become much more reflexed, especially at their lateral edges; the back of each lobe, which was originally convex, is now deeply concave like a boat, and the whole structure is in a manner turned inside out. The direction of the two divergent stigmas is at right angles to the two upper petals, and their tips point towards the median line of the two outer ones. In consequence of this arrangement the stigmas are at such a distance from the pollen on the lobes that no autogamy could take place without some special intervention. The requisite assistance is afforded by the two outer or inferior petals, and their mode of action is as follows. When evening comes the flower closes: the two lateral pollen-free lobes of each superior petal rise up first of all, and then the two inferior tri-lobed petals wrap themselves over them (see figs. 304³ and 304⁴). On the second or third day, when the margins of the pollen-laden lobes have curled back, contact ensues between the two closed petals and the revolute

margins of these lobes, and some of the pollen sticks to the petals, so that next day when the flower opens again a streak of pollen may be seen along the middle line of each of the outer petals (see fig. 304⁷). On the last day of bloom the two stigmatic arms curve down, and when the flower closes once more at dusk, they, being directed towards the median lines of the outer petals, are brought into contact with the pollen adherent along those lines (see fig. 304⁹), and thus at the last moment autogamy is effected.

The flowers of the Venus's Looking-glass (*Specularia speculum*, see figs. 304^{10, 11, 12, 13, 14, 15}) are protandrous like those of the common Bell-flower (*Campanula*); their anthers form a tube in the newly-opened flower (see figs. 304¹⁰ and 304¹¹), dehisce inwards and deposit the whole of their pollen on to the delicate hairs which clothe the external surface of the stylar column. When the tube of anthers breaks up through the shrivelling of their empty lobes, an axial column covered with pollen is exposed to view, and is used by insects as an alighting place. For the present pollen can only be taken away—not deposited—by insects, for the style-arms are still united, and the receptive tissue is inaccessible. Every evening the erect basin-shaped corolla folds up longitudinally in such a manner as to form five re-entrant angles (see fig. 304¹³). The in-folded angles of the corolla reach inwards as far as the central column (see fig. 304¹⁴), and get besmeared with some of the pollen with which it is coated. The next morning when the corolla opens linear streaks of pollen may be seen upon its internal surface. Meanwhile the three short arms of the style have disunited and spread themselves out, whilst the pollen has fallen off the stylar column (see fig. 304¹⁵), or been carried away by insects. If at this stage insects alight on the divergent style-arms fresh from visiting younger flowers, cross-pollination is certain to ensue. As night approaches the flower closes in the same way as on the previous evenings, and the pollen sticking to the lines of the internal folds comes against the style-arms, which are spread out and slightly reflexed (see fig. 304¹⁶), and thus effects self-pollination. In the event of the stigmatic tissue having already received a deposit of foreign pollen, this act of self-pollination is superfluous, but otherwise the process is effectual, and always results in the formation of fruit. A similar phenomenon may be observed in the nodding or pendent flowers of various Solanaceæ, particularly in the Potato plant (*Solanum tuberosum*), for here also there is frequently a transference of pollen to the corolla, and from the folds of the corolla to the stigma. But in this case the pollen issues from the anthers through terminal pores, and falls irregularly and not necessarily upon particular parts of the corolla, so that autogamy is not so certain to take place in these plants as in *Specularia*.

From the above descriptions it will be seen that in *Argemone*, *Hypocymn*, and *Specularia*, although the corolla is the part of the flower which is instrumental in effecting autogamy, the process does not involve any noticeable elongation of the pollen-besmeared corolla during the period of flowering. We have now to deal with another group of plants in which the petals perform just the same function as in the foregoing cases with respect to autogamy, but in which a very important part

of the operation consists in an elongation of the corolla. Types of this group are afforded by Gentianaceæ of the subdivision Cælanthe (*Gentiana asclepiadea*, *G. Pneumonanthe*, &c.), Liliaceæ (*Colchicum*), Amaryllidaceæ (*Sternbergia*), Iridaceæ of the genus *Sisyrinchium*, and those Composites whose capitula are furnished with ligulate florets (*Crepis*, *Hieracium*, *Hypochaeris*, *Leontodon*, &c.).

Gentiana asclepiadea (see fig. 305) is one of the sub-alpine species of the Baltic flora, and has protandrous flowers. The anthers are united into a tube, as in the case of Composites and Bell-flowers. They do not, however, discharge their pollen into the tube, but behave in this respect in the same manner as those of *Hypocoum*, that is to say, they open by longitudinal fissures down their external faces, so that after dehiscence the outside of the anther-tube is covered all over with pollen

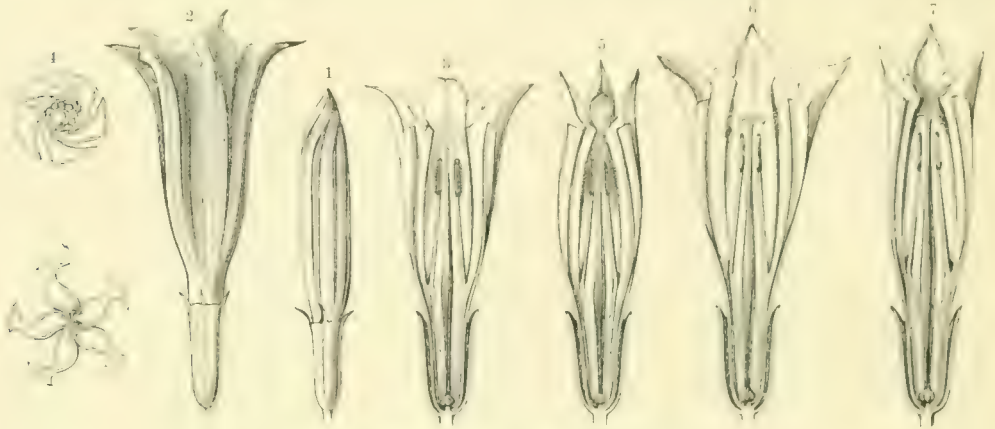


Fig. 305.—Autogamy effected by means of the corolla.

- ¹ *Gentiana asclepiadea*. Flower-bud shortly before it opens for the first time. ² Open flower in the last stage of development. ³ Longitudinal section through a flower which has just opened for the first time. ⁴ Transverse section through the same flower. ⁵ Longitudinal section through a flower closed for the first time. Pollen is affixed to the edges of the folds into which the corolla is thrown. ⁶ Longitudinal section through a flower which has opened for the last time. ⁷ Longitudinal section through a flower which has closed for the last time. The pollen is being transferred from the folds of the corolla to the reflexed stigmas. ⁸ Transverse section through the same flower. The anther-tube in ³, ⁵, ⁶, and ⁷ is represented in optical section.

(see fig. 305³). The linear style-branches bearing the stigmatic tissue are at this stage closely united and as yet immature. Humble-bees are attracted in large numbers by the rich store of honey in the floral interior, and as the funnel-shaped corolla is wide open in the daytime the insects enter, and are often entirely engulfed in the flower. If the visit is paid to a young, newly-opened flower the insect loads itself with pollen by coming into contact with the tube of anthers. Two days later the linear stigmas separate and curve over downwards. Their position now renders it inevitable that they should be touched by the bees, of which a large number continue to visit the flower, there being still plenty of honey in it. If these visitors have recently visited younger flowers they are sure to effect cross-fertilization. The corolla is disposed in peculiar folds, as is shown in figs. 305¹ and 305²; to describe them sufficiently briefly for our present purpose would not be possible. When the flower expands in the morning these plaits open out; at sunset they are again drawn in towards the middle of the funnel, and at the same time a movement

of torsion takes place which brings the folds into the position shown in transverse section in fig. 305⁴. The re-entrant angles come into direct contact with the surface of the anther-tube (see figs. 305⁴ and 305⁵) and take from it some of the pollen, which is very adhesive. On the next day, and on the third and fourth days, the flower opens and shuts again. During that time almost every part of the flower grows in length; the filaments gain 1 mm., the pistil 3 mm., and the inferior half of the corolla as much as 5 mm. In consequence of this growth the pollen transferred to the folds of the corolla from the anther-tube is raised 5 mm., and rests at the same level as the stigmas, which have in the meantime become divergent. When darkness sets in, and the corolla once more falls into folds and closes up, the pollen affixed to the re-entrant angles is transferred to the stigmatic tissue. The process is greatly facilitated by the fact that, at this final stage of flowering, the internal folds assume a somewhat different form and position (see fig. 305⁶), for in consequence of this change the parts besmeared with pollen are brought still nearer to the middle of the flower. This marvellous contrivance for promoting autogamy may also be observed in *Gentiana Pneumonanthe*, a species which grows in damp meadows in England and all over the continent of Europe, and in this instance the elongation of this funnel-shaped portion of the corolla in the interval between the first and last occasions of the flower's closing amounts to some 7 mm.

The phenomenon occurs in a much simpler form in *Sternbergia* and *Colchicum*, belonging to the orders Amaryllidaceæ and Liliaceæ respectively. The flower of *Sternbergia lutea* has an erect funnel-shaped perianth composed of six segments, three of which are rather longer than the other three. The six upright stamens have nectar secreted at their bases, and are adnate to the segments of the perianth; they are arranged in two whorls round the styles, and have their anthers turned outwards. The styles rise up in the middle of the flower in the form of three long threads. The stigmas, in which the styles terminate, are higher than the anthers throughout the period of bloom, and as, after the dehiscence of the anthers, the pollen adheres to the internal walls of the loculi, it is not spontaneously transferred to the stigmas in the same flower. The flowers are protogynous, and at the commencement of their bloom are adapted to cross-pollination through the agency of insects. Even after the extrorse anthers have dehisced, insects entering the blossom in quest of honey brush first against the stigmas, and only subsequently come into contact with the anthers resting at a lower level. The perianth is open in the daytime alone; in the evening its segments close together so tightly that their inner surfaces touch the extrorse anthers and become smeared with pollen. This happens the very first evening following on the dehiscence of the anthers. The pollen affixed to the perianth-segments does not reach the level of the stigmas till the following day. Its ascent is due to an elongation of the lower regions of the perianth-segments. There is a simultaneous growth of the other parts of the flower, but it is surpassed by the extraordinary increase in the length of the perianth-leaves. Whilst the styles grow 4 mm., and the stamen-filaments from 9 to 10 mm., these segments grow 18.5 mm. Afterwards, when the

perianth closes for the night, the pollen is transferred from the inner faces of its segments to the stigmas. Two subsidiary circumstances co-operate in bringing about this act of autogamy. The first is, the fact that the free extremities of the styles which bear the stigmatic tissue curve outwards when the flower's end approaches, and the second is, the circumstance that the excessive elongation is especially marked in the three perianth-segments which are opposite the stigmas.

The same events take place in the flowers of the Meadow Saffron (*Colchicum autumnale*). Anyone crossing a meadow in the autumn in which this plant is growing may see what a great difference exists between young and old flowers in respect of the length of the perianth-segments, and can easily convince himself of the connection between this diversity and the operation of autogamy as explained above. In the Meadow Saffron the phenomenon is somewhat complicated by the circumstance that heterostylism (see p. 302) plays a much more important part in this instance than in the other Liliaceæ. *Colchicum* possesses long-styled, mid-styled, and short-styled flowers, which all grow promiscuously together in one and the same meadow, and the elongation of the perianth-segments is anything but uniform in these three forms. Careful measurements of some five hundred specimens gave the following remarkable result. In long-styled flowers the three longer perianth-segments grow 9 mm. and the three shorter 12·6 mm.; in short-styled flowers the longer segments grow 10 mm. and the shorter 15 mm., and in the mid-styled flowers the longer segments grow 13·5 mm. and the shorter 18·5 mm. I shall return to the subject of heterostylism again presently, and shall then have an opportunity of entering more fully into its significance; at present it is only necessary to mention that the stigmas of the short-styled flowers, when the latter are nearly over, come into contact not only with the pollen sticking to the perianth-segments, but also with the tips of the anthers themselves, for in this form there is a proportionate growth of the filaments.

This same process, which in *Colchicum autumnale*, in Sternbergias and in Gentians of the Oenanthæ tribe only culminates in autogamy after the lapse of a week, is accomplished in the delicate plant *Sisyrinchium* of the order Iridaceæ in the course of a few hours. Apart from their ovaries, which are inferior, the flowers of *Sisyrinchium* are constructed similarly to those of Liliaceæ. The three small petaloid stigmas, in which the styles terminate, project above the anthers. The latter are coherent into a tube and open extrorsely, whilst the flower is still in the bud state, and the consequence is that some of their pollen is affixed to the contiguous leaves of the perianth. The flower opens out into a cup, and insects may then cause heterogamy; but on the approach of evening the perianth closes again, and autogamy takes place owing to the fact, that in the course of those few hours the petals have lengthened exactly enough to bring the pollen sticking to their inner surfaces to the level of the stigmas.

Reference must also be made to those Composites in which autogamy is brought about by means of an elongation of the ligulate corolla, and the consequent uplifting of the pollen adherent to it. In most and probably in all species of *Crepis*, *Hiera-*

cium, *Leontodon*, and *Hypochaeris*, in whose capitula the peripheral ligulate florets are considerably longer than those of the centre, it is easy to see that when the capitula close in the evening the ligulate petal in each flower rises up and lays its inner surface upon the pollen which has been extruded from the tube of anthers in the course of the day. The pollen remains sticking to the petal during the two succeeding days, and in the meanwhile the latter grows about a couple of millimetres in length and carries the pollen up with it. At the same time the style undergoes elongation and protrudes out of the top of the tube of anthers, holding its two arms, which are now divergent and expose the receptive stigmatic tissue



Fig. 306.—Autogamy effected by means of the corolla.

¹ *Pedicularis incarnata*. ² A flower of *Pedicularis incarnata* which has just become accessible to insects. ³ Longitudinal section through the same flower. ⁴ The same flower in a later stage of development. ⁵ Longitudinal section through the flower of ⁴. ⁶ The same flower shortly before the corolla fades; the upper lip is bent down and the mealy pollen falling out of the loosened valves of the anthers is trickling through the tubular upper lip upon the stigma stationed in front of the mouth of the tube. ⁷ Longitudinal section through the flower of ⁶. ¹ nat. size; the other figures double their nat. size.

upon their surfaces, at the same level as the pollen sticking to the ligulate corolla. When next the capitulum closes, the pollen is transferred to the stigmas, and autogamy ensues. This adaptation of the marginal florets of the capitula is all the more interesting, seeing that in the central florets in the same plants, geitonogamy has been found invariably to prevail (*cf.* p. 319).

One of the most curious contrivances for effecting autogamy consists in a special inflection of the corolla, on the termination of the flower's period of bloom, enabling it to conduct the pollen which falls from the anthers to the stigmas. The pollen in these cases is of mealy consistence. Two species of the Lousewort genus (*Pedicularis*) may be used to illustrate this form of adaptation, and we will first take

Pedicularis incarnata (see fig. 306), a species which grows abundantly in Alpine meadows. The flowers of this plant are arranged in spikes, and their development proceeds from below upwards (fig. 306¹). The corolla is bilabiate; the lobes of the under lip are at first upturned (see fig. 306²), but subsequently are expanded in a slanting plane (figs. 306⁴ and 306⁶). The upper lip is helmet-shaped and rolled into a tube at the apex (figs. 306^{2,3,4,5,6,7}). The stamens are of the sugar-tongs type, and their anthers are concealed underneath the arch of the upper lip (figs. 306^{3,5,7}). The long style is bent at an angle to correspond to the form of the upper lip; its anterior extremity passes through the tube and rests in front of the orifice and at the same time in front of the entrance to the floral interior. The humble-bees which make use of this entrance are obliged to rub against the stigma, and if they come laden with pollen from other flowers cross-fertilization ensues. Owing to the fact that the flowers are protogynous insect-visitors cannot, in the first stage of bloom (figs. 306² and 306³), carry off any pollen, but can only leave behind upon the stigma what they have brought with them; at later epochs, however, the insects, though still brushing first against the stigma, are next moment besprinkled with the mealy pollen which falls from the anthers in consequence of the disturbance of the tongs-like stamens. Under the galeate arch of the upper lip there is a slit (fig. 306⁴) to allow the pollen to fall freely, and whenever an insect enters between the under and upper lips this gap is enlarged. The head is the part of the humble-bee that receives the pollen, and the latter may, of course, then be conveyed to other flowers. If no insects visit a flower, the pollen remains for rather a long time dormant in the anthers; but, in the last stage of bloom, the filaments become flaccid and give way, and the pollen then falls of itself upon the edges of the slit. At the same time the upper lip undergoes a marked downward bending (fig. 306⁶), whereby that part of it which is prolonged into a tube, is brought into a vertical position, so that the pollen rolls down it, and is directed on to the stigma, which hangs right in front of the mouth of the tube (fig. 306⁷). Sometimes the stigma is drawn into the tube in the process of bending above referred to and sticks there, like a cork in the neck of a bottle; in which case self-pollination takes place inside the tube. Autogamy of the type exhibited in *Pedicularis incarnata* occurs with slight variations in all species which have the upper lip of the corolla produced into a tubular beak. The cases of this kind especially subjected to investigation were *Pedicularis asplenifolia*, *P. Portenschlagii*, *P. rostrata*, and *P. tuberosa*.

Very different behaviour is observed in several species of the same genus in which the upper lip has the form of a cowl or a helmet truncated in front, as, for example, *Pedicularis Ederi*, *P. foliosa*, *P. comosa*, and *P. recutita*. Of these we will take for illustration *Pedicularis Ederi*, which grows abundantly in Alpine meadows in the neighbourhood of the Brenner Pass in Tyrol. As regards the construction of its flowers, this species differs from *P. incarnata* in that the stigma is stationed in front of the truncated helmet forming the upper lip, and also in having projecting ribs on both sides of the corolla, which act like a system of levers in causing the inflection just before the flower fades. The entire upper lip at this

stage bends down so sharply as to look as if the flower had been wilfully broken. The back of the upper lip, which originally constituted a direct prolongation of the corolla-tube, now forms with it an angle of 60° , and later an angle of 90° . The movement is shared, of course, by the style and by the tongs-like stamens concealed beneath the upper lip. The consequence is that the stigma at the end of the style is no longer in front of the anthers, but underneath them, and that the anthers, which hitherto have been held tightly together, move asunder and let their pollen fall. The stigma is situated in the line of descent of the pollen, and, being very viscid, it catches a quantity of the particles of the shower, and thus secures the accomplishment of autogamy (cf. fig. 276, p. 272). The same changes of position, which, spontaneously initiated at the close of the flowering period lead to autogamy, may, curiously enough, be brought about at an earlier stage by the humble-bees which fasten on to the flower, but in that case they result in cross- and not self-fertilization. For a description of the processes involved the reader is referred to the account of them given on p. 272, where *Pedicularis recutita* is the species dealt with. We may here remark that the whole of the pollen which falls from the anthers in the last stage of flowering is not devoted to autogamy; the few pollen-cells which stick to the viscid stigma are sufficient for that purpose. A larger number of pollen-cells fall past the stigma into the air, where they may be caught up by a gust of wind, and carried away in the form of a tiny cloud of dust. If mature stigmas of other *Pedicularis*-flowers happen to lie in the direction in which the dust-cloud travels, individual cells of the cloud are left behind on these stigmas, and cross-fertilization thus ensues in the same way as in the flowers of the Toothwort (see p. 330).

Of the Rhinanthaceæ most nearly allied to the genus *Pedicularis* a few species of the Cow-wheat, which may be represented by *Melampyrum sylvaticum*, remain to be mentioned as instances of plants exhibiting the form of adaptation above described. The sole difference is that in *Melampyrum sylvaticum* the tube of the corolla bends at a sharp angle at a point only 2 mm. above the base, whilst the limb itself, composed of the lips, undergoes no independent flexion. The result is the same as in those species of *Pedicularis* of which an account has been given, inasmuch as the pollen falls, in consequence of the inflection, from the anthers of stamens of the sugar-tongs type on to the stigma beneath.

A kindred process to the preceding consists in the anthers with their coating of pollen being brought into contact with the stigma by means of an inflection of the corolla. The pollen is not mealy in this case, but adhesive. No one who will take the trouble to examine the inflorescence in one of the twining species of Honeysuckle (*Lonicera Caprifolium*, *L. Etrusca*, or *L. Periclymenum*) can fail to notice that the corolla-tube, in buds which are about to open, ascends in an oblique direction, that in newly-opened flowers it is horizontal, and that, a short time before a flower fades, it is bent downwards. The angle through which the axis of the flower is displaced relatively to the flowering stem varies from 45° to 90° ; in the case of horizontal stems it is less, and in that of erect stems greater, but the object invariably aimed at is that the open corolla shall, as night comes on, be disposed in

the most convenient manner possible for nocturnal moths to visit it. In flowers adjusted in anticipation of such visits, the stigma takes up a position which precludes the possibility of its being dusted with pollen from the anthers in the same flower. In the act of introducing their long probosces into the honey secreted in the interior of the flower, Sphingidæ come into contact first with the stigma and then with the anthers, and as they travel from flower to flower they are the means of effecting cross-pollination in this as in so many other cases. But should no moths come upon the scene, autogamy invariably takes place through the inflection of the corolla-tube already referred to. The stamens are adnate to the corolla-tube, and undergo inflection with it, thus bringing the anthers, still covered with pollen, into direct contact with the stigma, which, in the horizontal position of the flower, was stationed a little lower than, and in front of, the anthers.

In respect of the manner of their autogamy the last-mentioned plants exhibit a transition to a large group in which self-fertilization is prevented during the early stages of flowering by the relative positions of anthers and stigmas, but is effected towards the end of the period of bloom, when certain changes in the position and direction of the *flower-stalks* have taken place and brought the pollen and stigmas into conjunction. These alterations of position are usually associated with one of the many other contrivances already described. Thus, for instance, the styles or the filaments may undergo elongation and inflection, or the corolla may grow up and carry with it pollen affixed to its petals, or the stamens themselves, and so forth; but these processes would not of themselves be sufficient to induce autogamy if it were not for the part played by the flower-stalks. To put it briefly, the stigmas and the anthers become, in the absence of cross-fertilization, so situated by the growth and inflection of the flower-stalk as to render autogamy inevitable. When we consider that the changes in the position and direction of pedicels, and the consequent drooping or straightening up of flowers, serve other purposes of great importance in the life of plants, and that, in particular, to these inconspicuous movements are often due the protection of pollen from moisture and the placing of the entrance to a flower in the position most convenient to insects whose visits are profitable to the plant, we cannot be surprised to find that this form of adaptation is one of the commonest of all. A combination of advantages, either simultaneous or in rapid succession, is secured, and contrivances of this kind which best contribute to the economy of plant-life are found by experience to be invariably the most widely distributed.

We will first consider flowers in which the stigma begins by being situated outside the line of descent of the pollen as it falls from the anthers—a circumstance which is advantageous inasmuch as it favours cross-fertilization—but where subsequently the entire flower assumes a different position in consequence of a growth or an inflection of the flower-stalk, whilst the direction and situation of stamens, style, and stigmas remain the same as before. In several species of *Narcissus*, e.g. the graceful *Narcissus juncifolius*, and in some Boraginæ, such as the common Wood Forget-me-not (*Myosotis sylvatica*), the flowers at first have their mouths set

in a lateral direction; the stigma is stationed behind the anthers, and the pollen that falls out of the anthers does not come upon the stigmas so long as the corolla-tube is horizontal. During that period the branch of the inflorescence to which the horizontality of the corolla is due is curved, but it subsequently straightens out and raises the corolla-tube to a vertical position whereby the stigma is brought into the line of descent of the pollen as it falls from the shrivelling anthers. This occurs in *Tulipa sylvestris*, *Polemonium caruleum*, *Saxifraga hircifolia*, *Chrysosplenium alternifolium*, *Rhododendron Chamæcistus*, *Vaccinium*, *Arctostaphylos*, *Cerinth*, *Symphytum*, and *Cyclamen*. The process may be most clearly traced in the various species of *Cyclamen*, which are at present so commonly grown in pots. The first day that the flower is open and the petals reflexed, the peduncle, which rises up from the ground, has its extremity bent over almost at a right angle. The short bent piece of the stalk is inclined at an angle of from 50° to 60° to the horizon. The variation in the size of the angle is due to the fact that the longer inferior part usually ascends obliquely from the ground, and is only in rare cases quite vertical. From day to day the angle of inclination may be seen to diminish by about 10° until at the end of the flower's period of bloom the short down-bent portion at the top and the long upright portion of the peduncle are almost parallel, and the whole has the form of a crook. As the style lies in the direct line of prolongation of the short piece of the peduncle and projects beyond both the tube of the corolla and the cone of anthers, autogamy cannot take place in the first stage of the flower's development, when the style is inclined at an angle of from 50° to 60° to the horizon. Insects visiting the flower at this period first brush against the stigma at the end of the projecting style, and may occasion cross-fertilization; but even if it should happen that the displacement of the anthers caused by an insect's intrusion has the effect of letting some of the pollen fall out, the shower does not descend upon the stigma, for it is not yet situated vertically beneath the anthers. Towards the close of the flowering period, on the other hand, the stigma is moved by means of the inflection of the peduncle above referred to into the path along which the pollen descends; the filaments become flaccid, the anthers disunite, and the pollen stored in the cone is sprinkled upon the still receptive surface of the stigma.

This will be the best place to describe the curious case of autogamy which is exhibited by the *Calceolaria Paronii* of South America. The flowers of this plant are protogynous, and when first open they are borne on almost horizontal stalks. The anthers, which are still closed, are concealed beneath the shortly truncate upper-lip. The style bearing the already mature stigma is borne horizontally, its tip only being bent down like a hook at a short distance from the stigma (as is shown in figs. 307¹ and 307²) so as just to touch the roof of the inflated under-lip. The short-tongued Hymenoptera which come in quest of the honey secreted within the lower-lip make use of its roof as an alighting-place. The instant one of them settles upon it the lip drops as in the case of the Snapdragon, the movement being regulated by the powerful ribs on each side of the corolla. The result is

twofold: the jaws of the flower are set wide open and the honey-secreting lobe hitherto concealed in the hollow of the lip is brought out so as to enable the insect which has caused the movement to lick up the honey without difficulty. In doing so, however, it rubs its back against the stigma, and should it have previously visited older flowers cross-pollination ensues. These are the conditions at the commencement of flowering. The next day or the day after that, the anthers open by comparatively large pores, one at the top of each loculus. The connectives

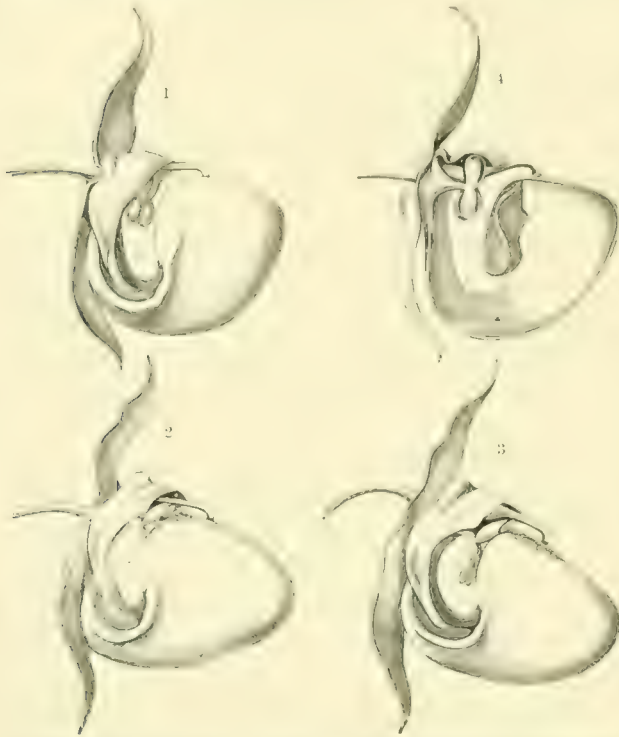


Fig. 307.—Autogamy caused by inflection of the flower-stalk and the adjustment of the under lip to form an inclined plane down which the pollen deposited upon the under-lip slides to the stigma: *Calceolaria Pavonii*.

1, 2, 3 Side view of the flower in the three successive stages leading to autogamy. 4 Longitudinal section through a flower in the first stage of development. All the figs slightly magnified.

are articulated to the filaments, so that when the latter are pushed the anthers are set swinging and let fall some of their mealy pollen. If under these circumstances a rather large Hymenopter alights on a flower in quest of honey, he must necessarily knock against the filaments and be sprinkled by the pollen which descends in consequence, especially seeing that the filaments have meanwhile increased in length sufficiently to bring the upper lobes of the anthers upon the highest part of the arched external surface of the under-lip. If the flower is not visited by insects, a quantity of the mealy pollen falls of itself upon this convex surface (see fig. 307²). Soon afterwards the flower-stalk

curves down, causing a steep inclination of the roof of the under-lip, which still bears on its highest part the heap of pollen deposited by the anthers. The pollen slips down the inclined plane, and is thus brought into contact with the stigma, which still retains its receptive power (see fig. 307³).

The accomplishment of autogamy, by means of a combination of movements and inflections of the flower-stalks with similar action on the part of the stamens and style is of as common occurrence as it is varied in respect of details. The drooping Star of Bethlehem (*Ornithogalum nutans*) derives its name *nutans* from the attitude of its flowers, but the latter really do not assume that position until quite at the last; in the bud-stage they are erect, and even after the leaves

of the perianth have expanded the pedicels stand out horizontally from the axis of the inflorescence, and the flowers face sideways. The flowers are protandrous. The anthers of the three stamens, situated in front of the little pits in the ovary in which honey is secreted, dehisce at the same moment as the perianth-leaves expand, and these anthers are placed in such a position as to be touched by insects as they enter the flower. The stigma is still immature at this stage. A little later, when the stigmatic tissue has developed the power of retaining pollen, the stamens move out of the way of insects towards the periphery of the flower and thus render it possible for cross-pollination to be effected by such of these visitors as bring with them pollen from younger flowers. In the third stage of the flower's duration the pedicel bends down until the flower is at last truly nodding. The stamens have meantime executed a reverse movement towards the middle of the flower, and the stigma is found to be just underneath one of the anthers belonging to a stamen of the shorter class. These anthers always have some pollen left in them, for they do not open till the second stage of the flower's development and cannot have undergone contact with insects. The gradual shrinkage of the anthers now causes this store of pollen to fall out of them on to the adjacent stigma, and thus autogamy is effected just before the flower fades.

The hermaphrodite flowers of certain Rosaceæ — *Dryas octopetala*, *Geum coccineum*, *G. montanum*, *G. reptans*, *Potentilla atrosanguinea*, *P. repens*, and *Waldsteinia geoides*—and those of some Ranunculaceæ, viz., *Adonis vernalis*, *Anemone alpina*, and *A. baldensis* afford particularly instructive examples of autogamy. In all these plants the flowers are protogynous and are characterized by having a large number of carpels crowded together in the centre and surrounded by equally numerous stamens, which are disposed in several whorls. In the Rosaceæ in question the stamens are tucked down before the bud unfolds, and they do not straighten out until the anthers are nearly ready to open. Dehiscence occurs first in the anthers which belong to the outermost whorl of stamens, and are furthest away from the stigmas of the bunch of ovaries in the middle. This relative position of the two sets of organs excludes all possibility of autogamy, especially when the flower is erect; on the other hand, cross-pollination is quite likely to be effected by insects, which alight on the stigmas, thence proceed towards the circumference of the flower, licking up honey and collecting pollen on the way, and finally take wing from the edge to visit other flowers. By degrees, the stamens of the innermost whorl come to maturity; they straighten out and elongate, and their anthers with pollen exposed upon them are brought to the same level as the stigmas of the central pistils. A transference of pollen to some of these stigmas is now certain to ensue, and is rendered all the more inevitable by the outward inclination and inflection of the styles belonging to the pistils most remote from the centre which now take place, and bring the corresponding stigmas into direct contact with the pollen. But if this were all, the stigmas in the centre might get no share of pollen in the event of an absence

of insect visitors. To obviate this possibility the flower-stalk bends in a gentle curve to one side so as to bring the last-mentioned stigmas into the line of descent of the pollen when it falls from the anthers at the end of the flowering-period. The process in the Ranunculaceæ referred to only differs from that just described in trifling respects. In *Adonis vernalis* no outward inflection of the style can take place on account of its shortness, but on the other hand the stamens nearest to the ovaries curve inwards and deposit their pollen upon the adjacent stigmas. In *Anemone alpina* the anthers of the innermost whorl of stamens are the first to open, and the order of development is from that whorl outwards. Owing, however, to the fact that the styles are crowded close together in a dense tuft at that earliest stage, autogamy is not effected at once; later on the styles become bent and twisted, and some of the stigmas touch the anthers in consequence; and when in addition the pedicel undergoes inflection and causes the flower to nod, the rest of the stigmas are brought vertically under the anthers and catch the pollen which falls from them. In *Pyrola uniflora* (see fig. 308²), a native of fir-woods, autogamy is brought about at the close of the flower's period of bloom by means of a marvellous co-operation of the stamen-filaments and the flower-stalks. The bud about to open (see fig. 308¹) and the young flower whose petals have just expanded (see figs. 308² and 308³) are borne on stalks which are strongly curved, and they are thus inverted and pendent. The style is vertical, with the stigma pointing downwards. The filaments are S-shaped and hold the anthers, which are of the pepper-caster type, with the two pores invariably uppermost so that the pollen does not fall out of itself or at any rate cannot come upon the stigma (fig. 308³). Insects approaching from below brush first against the stigma and directly afterwards against the anthers which are in consequence upset, and besprinkle the intruders with pollen. This pollen is then carried to other flowers of *Pyrola uniflora*, where it is retained by the viscid stigmas and fertilizes the ovules. During the period of bloom two changes are effected, which though not very striking in themselves are yet of extreme importance with a view to autogamy. In the last stage of the flower the curve of the pedicel no longer amounts to a semicircle, and consequently the flower is no longer absolutely pendulous but only facing obliquely down (fig. 308⁴); the style is no longer vertical, but with this new position of the flower points also obliquely downwards and the stigma is thus brought underneath some of the anthers. The filaments are still curved in the shape of the letter S but in the opposite direction to that held by them at the commencement of the flowering-period (cf. figs. 308³ and 308⁵); the anthers are therefore inverted and have their pores directed downwards. The least shaking of the slender stem by the wind is now sufficient to cause a fall of pollen, and, in its present position, the viscid stigma cannot fail to get sprinkled with some particles from the shower which descends on such occasions (see figs. 308⁴ and 308⁵).

In *Phygelys capensis*, a plant belonging to the Scrophulariaceæ of the Cape, and also cultivated elsewhere in gardens for the sake of its deep scarlet flowers, the branches of the inflorescence and the pedicels stand out nearly horizontally from

the stiff upright stem (see fig. 309¹). The pedicels are thickened just where they pass into the flowers and bent down so as to hold the flowers, when they are newly open, approximately at right angles to their stalks, which gives a curious appearance to the inflorescence as a whole. The flowers are protogynous, and, on the first day that they are open, the stigma can only be dusted with extraneous pollen from older flowers. The style is originally curved, so that the receptive tissue is held in front of the entrance to the floral interior where honey is abundantly secreted, and in this position it is inevitably brushed against by insects visiting the flower (fig. 309¹,



Fig. 303.—Autogamy caused by the combined inflections of pedicel and stamen-filaments: *Pyrola uniflora*.

- ¹ Longitudinal section through a bud about to open. ² The whole plant with its flower in the first stage of development.
³ Flower in the first stage of development slightly magnified; the front petals are cut away. ⁴ The entire plant with its flower in the last stage of development. ⁵ Longitudinal section of a flower in the last stage of development; slightly magnified.

the right-hand flower). The next day the style straightens out, and the stigma is consequently moved away from the passage to the honey, whilst, on the other hand, the anthers open and place their pollen-coated faces exactly in the path of insects coming in search of honey (fig. 309¹, the middle flower). On the third day the style becomes curved again and takes up the same position as it occupied on the first day. At the same time the pedicel undergoes further inflection and brings the tubular corolla nearer to the main axis of the inflorescence (fig. 309¹, the left-hand flower). The result of these combined inflections is that the viscid stigma is brought right under the anthers at the time when they are shrivelling and catches a portion of

the crumbly pollen as it falls from them. Even if the pollen does not fall upon the stigma autogamy does not fail; for the corolla slips along the style as it drops, and is certain to touch both anthers and stigma, and to transfer to the latter the last grains of pollen adhering to the anthers (see fig. 309²).

Reference has often been made in former chapters to the splendid creeper named *Cobaea scandens*, one of the Polemoniaceæ native in tropical America, but capable of thriving luxuriantly in the gardens of Central and Southern Europe, where it is used for clothing espaliers, which it covers in the height of summer with deep-purple bell-shaped flowers (see fig. 310¹). The anthers are borne on long filaments with hairy bases, and are situated, at the commencement of the flowering-period,

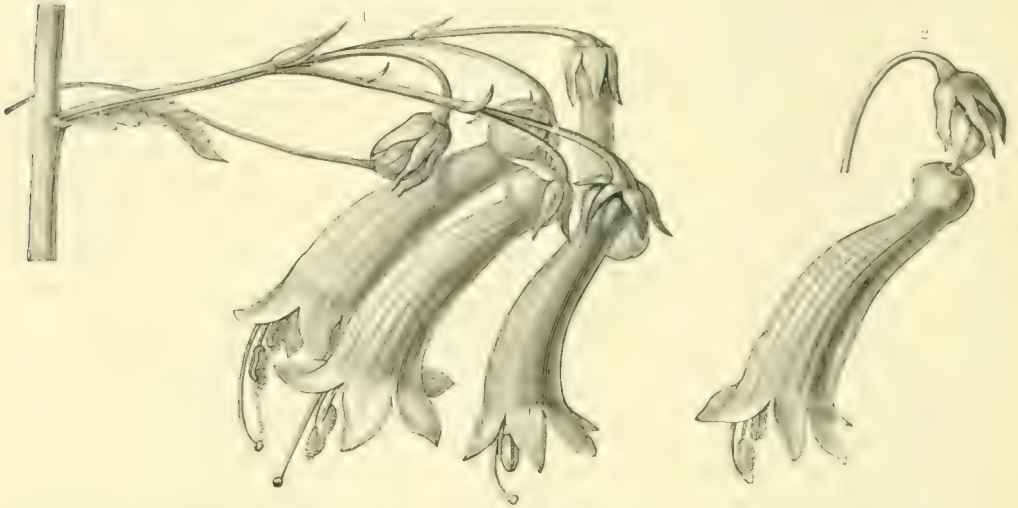


Fig. 309.—Autogamy ensuing in consequence of the inflection of the pedicel and the disarticulation of the corolla: *Phygellus capensis*.

¹ Portion of an inflorescence; the flowers borne by a horizontal branch of the inflorescence in the successive stages of development leading to autogamy (from right to left). ² A single flower at the moment of the detachment of the corolla and the rubbing of the anthers against the stigma.

right in the mouth of the flower, where they are certain to be touched by insects which enter the flower to get the honey. The style is still short at this stage, and has its free extremity concealed under the anthers, whilst the three terminal branches of the style which bear the stigmatic tissue are closed tightly together (see fig. 310²). A little later anthers and stigmas change places; the filaments elongate and twist themselves into the form of corkscrews, and the anthers then rest lower than the three style-arms, which diverge and place themselves in a position to receive pollen brought by insects from younger flowers (see fig. 310³). If no insects make their appearance, and there is consequently no cross-fertilization, the pedicel undergoes inflection to the extent of about 45°, and the flower, hitherto nodding, becomes completely pendent. At the same time the style curves, and the coils of the stamen-filaments are drawn closer together. The result of all these movements is that the anthers are brought into contact with the stigmatic tissue, which is still receptive, and autogamy ensues (see fig. 310⁴).

Allium Chamæmoly (see fig. 311¹) is an example of the plants, in whose flowers autogamy is effected by concurrent movements of the pedicel and the style, the former undergoing inflection, whilst the latter is inclined in the direction of the spots where the pollen has been deposited. The small white flowers are lifted but a very little way above the ground; at first they face the sky, and are half hidden amongst the long green ribbon-shaped foliage-leaves. Nevertheless, they are assiduously sought out by small insects, the honey, which is secreted in little depressions on the surface of the ovary, being in great request. During the first stage of flowering cross-pollination alone is possible; the stigma is posted in the middle of

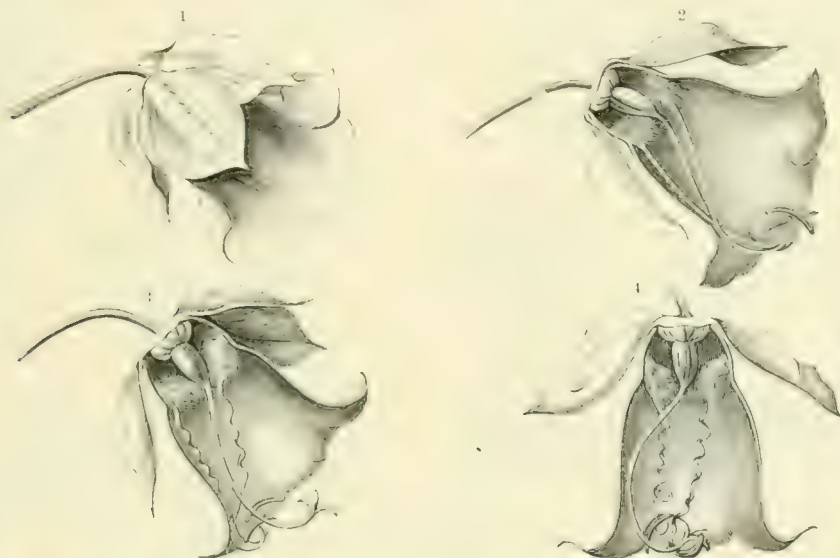


Fig. 310.—Autogamy resulting from an inflection of the pedicel accompanied by spiral torsion of the filaments: *Cobaea scandens*.

¹ Side view of a newly opened flower. 2, 3, 4 Flowers in the three successive stages of their development which lead to autogamy. All the figs. somewhat reduced.

the mouth of the flower, and its tissue is already receptive whilst the anthers are still closed and appressed to the walls of the perianth (see fig. 311²). Later on all the filaments undergo inclination towards the middle of the flower; the anthers burst open, become covered all over with the pollen which issues from their loculi, and together form a yellow knob which occupies the centre of the entrance to the interior of the flower, and is brushed by all intruding insects. The stigma is at that stage hidden behind the anthers (see fig. 311³), and is not touched by insects. If, for any reason whatever, insects do not visit a flower, autogamy takes place in the third stage of its development. The pedicel curves over downwards and presses the flower against the ground, and, as a consequence, the delicate white perianth-leaves and filiform stamens are displaced, and some of the pollen falls out of the anthers on to the lower perianth-leaves now resting upon the ground. The style undergoes slight lateral, *i.e.* in these circumstances downward, inclination and the final result of all these movements is that the stigma is brought into contact either with the

pollen lying on the lowest perianth-leaf or with that still sticking to one or other of the anthers (see fig. 311⁴).

Of the plants in which autogamy is brought about by inflection of the pedicel combined with inflection or folding of the *petals*, two groups will be taken here as representing two different forms of the phenomenon. These groups consist of the *Violacæ* of the *Melanium* tribe and the stemless Gentians. The manner in which the pollen is transferred to the stigma in Violets through the agency of insects has



Fig. 311.—Autogamy resulting from inflection of the pedicel combined with inclination of the style to the place where the pollen has been deposited: *Allium Chamæmoly*.

¹ Shows the aerial portions of the plant; nat. size. ^{2, 3, 4} Single flowers with the front perianth-leaves removed; slightly magnified. They are in the successive stages leading to autogamy.

been already described on p. 280, and illustrated in figs. 279^{1, 2, 3} on p. 279. The pollen thus deposited by insects on the slightly-projecting flap of the capitate stigma is derived, of course, from other flowers, and the result of its transference is a crossing between the flowers either of one or of two species. Autogamy is in general scarcely possible in the Violet during the first part of the flowering-period. If pollen is shaken out of the cone of anthers on to the proboscis of an insect which is in the act of dusting the front surface of the stigmatic lobe with foreign pollen, this new supply may, perhaps, be rubbed off on to the back of the stigmatic lobe as

the proboscis is withdrawn, but it does not even then come upon the receptive surface of the stigma. As regards the pollen which, though shaken out, is not carried away by the insect, but left lying underneath the cone of anthers in the trough of the spurred petal, it also does not reach the stigmatic tissue during the first stage of the flower's development, for the groove is still closed by the projecting lobe of the stigma. Towards the end of the flower's duration, however, the case is very different. The *Violas* of the *Melanium* tribe may be represented by the Field Pansy (*Viola arvensis*), it being the most widely-distributed species of the section. In these plants the cone of coherent anthers gradually breaks up of itself, and the pollen falls out, and fills the hinder part of the channel of the spurred petal. At the same time the lamina of this petal bends in such a manner that its trough is no longer closed by the stigmatic lobe, and the pollen is free to slip towards the mouth of the flower. The only condition now requisite is some change capable of setting the pollen in motion, and this is afforded by an inflection of the flower-stalk. Although the flower-stalk in the Field Pansy, Heart's-ease (*V. tricolor*), and other species of the *Melanium* tribe undergoes sharp inflection (see vol. i. p. 531) on clear nights, this movement has no influence in promoting auto-gamy at the time when the flower is in full bloom. At the last, however, it causes the mealy pollen to slip further and further down the groove in the lowest petal until it reaches the receptive stigmatic tissue.

There is a remarkable resemblance between this process and that observed to take place in those *Gentians* which are called by Descriptive Botanists "acaulescent" or stemless species (*Gentiana acaulis*, *G. angustifolia*, *G. Clusii*, see fig. 312). The flowers of these *Gentians* are of the type of "revolver-flowers" (cf. p. 250). The filaments are adnate to the lower part of the funnel-shaped corolla, and project in the form of five stout ridges towards the ovary, which appears as a column standing up in the middle of the flower: the ridges and the ovarian column, coming into contact with one another, divide the corolla into five tubular passages leading to the honey which is secreted abundantly at the bottom. The anthers are a little higher than half-way up the funnel of the corolla, and are connate into a tube which surrounds the style. Each anther dehisces extrorsely by two longitudinal slits, and immediately after the flower opens the anther-tube is covered all over with pollen. Above the tube is the stigma, which is composed of two notched and lacerated white lobes. The positions of the stigmas and anthers, respectively, ensure cross-pollination through the instrumentality of the humble-bees which fly from flower to flower. If, however, unfavourable weather prevails, and the bees stop away, the pollen gradually falls from the anthers as they shrivel, and is transferred to the stigmas in the same flower through the agency of the corolla and pedicel in the following manner. As long as the flower remains upright or ascends obliquely (see figs. 312¹ and 312²) the pollen falling from the shrinking anthers collects above the bases of the filaments, where they coalesce with the corolla, and when the corolla folds up for the night or to protect the pollen from rain, the pollen falls down between the folds, which, starting from close to the bases of the filaments, extend nearly to the

mouth of the flower. These furrows constitute, in fact, the channels through which the pollen is afterwards conducted to the stigmas. The only movements needful for the attainment of this object are the inversion of the flower, and the placing of the stigma in such a position that its fringed edges may reach to the furrows in question. Both these conditions are complied with. The inversion of the flower is brought about by a considerable elongation of the pedicel, which is very short when the flower first opens, and by its semicircular inflection at the approach of night and in wet weather (see fig. 312²). The introduction of the stigmatic margins into the furrows is due to the growth of the style, which carries the stigma up into the conical cavity formed near the apex of the flower when the corolla-limb folds up.



Fig. 312.—Autogamy resulting from inflection of the pedicel combined with the folding up of the corolla.

¹ *Gentiana Clusii* showing the flower as it is when opened for the first time. ² The same plant with its flower in the last stage of development, the corolla closed and the pedicel elongated and curved downward in a semicircle. ³ Longitudinal section through a newly-opened flower. ⁴ Longitudinal section through a flower which has closed for the last time.

All the furrows of the corolla-tube open into this cavity, and converge into such proximity to the axis of the flower that contact with the edges of the stigmatic lobes, which occupy the middle of the conical cavity, is inevitable. If, under these conditions, the drooping flower is shaken by drops of rain falling upon it, or by gusts of wind, the pollen slips along the smooth furrow right down to the stigma, and is caught by its fringed margins (see fig. 312⁴). It is worthy of note that *Gentiana acaulis*, *G. angustifolia*, and *G. Clusii*—the plants to which the above description applies—grow for the most part on grassy slopes, and on the ledges of precipitous rock-faces in the Alps; thousands of flowers of these species may be seen in situations of the kind with their heads drooping in wet weather so as to lie parallel to the slope of the ground, and fruits are invariably developed from these flowers, even after long-continued rain. On the other hand, flowers growing on flat

meadows sometimes have no opportunity of becoming nutant. In them, as might be expected, autogamy fails, and if the weather is bad, and no humble-bees are about, cross-fertilization may also be prevented; therefore it is not unusual to find many ovaries unproductive in level places of the kind.

The Pasque-flowers, *Anemone Pulsatilla* and *A. vernalis*, may be taken as representatives of the cases in which autogamy is achieved by means of an inflection of the pedicels combined with an elongation of the sepals. The flowers of these plants have very short stalks and face the sky when they first open. They remain in that position for about forty-eight hours, opening in the daytime when it is fine, and closing at night and when it rains. No drooping of the flowers is to be perceived during the first two days, and indeed such a change would scarcely be possible, considering the shortness of the stalks. The flowers are markedly protogynous. The stamens are crowded together in large numbers, and their closed anthers, grouped in the middle of the flower, resemble the grains of a head of maize. Above the anthers rises a sheaf of styles bearing mature stigmas. Insects, especially hive- and humble-bees, are attracted at this stage of floral development by the honey which is secreted by small club-shaped nectaries interspersed amongst the sepals and stamens. On entering a flower they rub against the sheaf of stigmas, even if they have not actually used it as an alighting-place, and, in the event of their bodies having been besmeared with the pollen of older flowers, a cross with some plant which may be either of the same or of another species ensues. When two days have elapsed, the aspect of affairs is altogether changed. The peduncle has become considerably longer, and the flower nods slightly when darkness sets in: the inner stamens are no longer stiff but curve outwards, whilst those anthers which are nearest to the styles have undergone dehiscence and offer their pollen for dispersion. The sepals, which are concave towards the middle of the flower, have elongated somewhat to protect the pollen. Insects now come in quest of pollen as well as honey, and are certain to get dusted with a quantity of it which they may then transport to other flowers. When a flower closes in the evening, pollen from the anthers of the reflexed stamens is invariably affixed to the inner surface of the superincumbent sepals. At this stage, too, pollen is liable to be shaken out of the anthers of the longest stamens, and this falls, in the case of a nodding flower, on to the central stigmas of the fascicle of styles. Two days later, again, the condition of the flower is as follows:—The stalk is from ten to twenty times as long as it was, and the flower is nutant in the daytime as well as by night. The stamens have all relaxed from their rigidity: the filaments are curved outwards, and the anthers are open. The sepals have more than doubled their original length, and the pollen affixed to their inner surfaces has consequently been raised to the level of the stigmas. In addition, the form of the three inner sepals has changed: the concave inner face is now convex, and the external surface is concave. The result of these changes is that the stigmas at the periphery of the fascicle now receive their share from the elongated sepals, which are appressed to them and yield up to their receptive tissue the pollen sticking to their inner surfaces.

The processes which lead to autogamy in the Water Avens (*Geum rivale*), the Raspberry (*Rubus Idæus*) and some other Rosaceæ allied to these are even more complicated than those above described. Thus, for example, the flowers of *Geum rivale*, on the day that they open, face laterally and have their stalks horizontal; the filaments are short, and the anthers are all closed, while the stigmas which project in a tuft 2 mm. beyond the anthers are already mature. At this stage insects may occasion cross-fertilization, but autogamy is not yet possible. Subsequently, the filaments lengthen and the anthers of the longest stamens open and come into contact with some of the stigmas at the periphery of the bundle of styles. The pedicel is now curved and the flower nods; consequently, the pollen which falls from the anthers above, when they shrivel, is forthwith received by the outer stigmas of the fascicle of styles, that is to say, by those of the outer stigmas which appertain to the upper half of the flower. The pollen which falls from the anthers of the under half of the flower when they dry up, is caught, on the other hand, by the petals on that side of the flower, and is afterwards transferred, by means of an elongation of these petals, to the stigmas of the adjacent reflexed styles. A couple of days later the pedicel is curved into a semicircle, and the flower hangs down with its mouth towards the ground. By this time the anthers of the shorter stamens are open; the whole flower has become loosened, and the fascicle of styles resembles a sheaf of corn. All the styles, including those in the middle, become twisted and reflexed to the extent necessary to bring the stigmas underneath the most recently opened anthers, and when these anthers shrivel and the pollen is forced out, it falls upon the central stigmas, which hitherto have not been furnished with any. Thus, in this case we have (1) the inflection of the pedicels, (2) the elongation of the petals, (3) the elongation of the stamens, and (4) the inflection of the styles—all co-operating towards the same end, namely, that in the event of no insects visiting a flower all the stigmas may receive pollen from the anthers developed in the flower itself.

The foregoing descriptions, though extremely brief and cursory, give a general idea of the many kinds of contrivances whereby autogamy, as well as heterogamy, is promoted in hermaphrodite flowers. It is evident from them that any mechanism which leads to autogamy has full scope for its operation only if cross-pollination has not previously been effected. Again and again we have found that certain processes only take place in the event of a flower being unvisited by insects through whose agency cross-fertilization would have been brought about. In this connection we have also the remarkable phenomenon that many flowers adapted to cross-fertilization by insects do not open at all when there is no chance of their being visited by the agents in question. In the mountainous districts of the temperate zones it often happens that rainy weather sets in just at the time when the flowers are about to open, and that it lasts for weeks. Humble- and hive-bees, butterflies, and flies retire to their hiding-places, and for a considerable time cease to pay any visits to flowers. The growth of the plants is not, however, arrested during this period, and even in the flowers themselves development quietly progresses if the

temperature be not too low. The stigmatic tissue becomes receptive; the anthers attain to maturity, dehisce and liberate their pollen notwithstanding that no ray of sunshine penetrates the clouds and that rain falls continuously. In such circumstances the mouth of the flower is not opened; autogamy takes place in the closed flower, and all the adjustments evolved with the object of ensuring cross-fertilization are ineffectual. This is the case, for instance, in the following:—*Alsine rubra*, *Anagallis phœnicea*, *Arabis cœrulea*, *Azalea procumbens*, *Calandrinia compressa*, *Centunculus minimus*, *Drosera longifolia*, *Gagea lutea*, *Gentiana campestris*, *G. glacialis*, *G. prostrata*, *Hypecoum pendulum*, *Hypericum humifusum*, *Lepidium sativum*, *Montia fontana*, *Oxalis corniculata*, *O. stricta*, *Polycarpon tetraphyllum*, *Portulaca oleracea*, *Sagina saxatilis*, *Silene noctiflora*, *Sisyrinchium anceps*, *Spergula arvensis*, *Stellera Passerina*, *Veronica alpina*, *V. bellidioides* and *V. Chamædryas*—plants which grow in widely different habitats, but which all have the common property that their flowers open for but a short period, if at all. In plants with long-lived flowers it is of not uncommon occurrence for autogamy to be accomplished during a spell of wet weather, and for the petals to open subsequently all the same, and so afford the possibility of the remains of the pollen being carried away by insects. This phenomenon has often been observed, for example, in *Rhododendron hirsutum*, the Bog-bean (*Menyanthes trifoliata*), and the Greater Dodder (*Cuscuta Europæa*).

There is also the case of such plants as *Alisma natans*, *Illecebrum verticillatum*, *Limosilla aquatica*, *Peplis Portula* and *Sabularia aquatica*, which live in pools or on the banks of ponds where the level of the water is variable. If the buds of these plants are submerged at the time when they are about to open, they do not unfold, and autogamy takes place in the closed flowers under water. It must be observed that the water does not penetrate into the air-filled interior of the flowers, so that we have here the curious phenomenon that the transference of pollen to the stigma, though accomplished under water, is yet a case of pollination in the medium of the air.

An allied phenomenon is exhibited by some of the Knotweeds (*Polygonum Hydropiper*, *P. minus*, and *P. mite*). Isolated plants of any of these species, in which all the flowering branches are exposed to the sunshine, and are both visible and accessible to insects, unfold all their flowers; but, if hundreds of one species are crowded close together, only a limited number of the flowers open their perianths. The flowers growing on the upright branches alone of such crowded plants unclosethemselves, and receive insects' visits, whilst those which grow on the under, procumbent branches, and are consequently concealed and not easily reached by insects, remain shut. Nevertheless autogamy is effected with obvious success in these also.

Plants of the kind just alluded to form a transition to those which normally produce two kinds of flowers, viz.: some which open and are adapted to cross-fertilization through insect-agency, and some which remain closed and exhibit autogamy with great regularity. The latter have received the name of *cleistogamic* (*κλειστός*=that can be closed, *γάμος*, marriage) flowers, and amongst them may be dis-

tinguished a series of very wonderful forms. A common characteristic of them all is the stunted development or complete abortion of petals which would otherwise attract insects by their scent, colour, or honey. The only function of the petals is that of an envelope under cover of which ovules and stigmas, anthers and pollen, attain maturity and are able to enter into combination with one another. In many cases there is no trace of a corolla to be seen; green sepals alone are developed into a floral envelope, and they are kept fast closed and cover the stamens and pistil in the form of a hollow cone. Thus, for instance, *Aremonia agrimonioides*, a plant growing abundantly in the forests of Carniola, has cleistogamous flowers about a millimetre in diameter, in which stamens and sepals spring from the edge of the excavated disc, whilst petals are entirely absent. In other cases, though petals exist, they remain small and of a greenish-white tint. Precisely those parts of the corolla which in open flowers are most conspicuous in form and coloration are here abortive. Thus, in the cleistogamous flowers of several species of Violet, the spurred petal, which in the open flower is the most striking, is scarcely recognizable: its lamina is oval in outline, and is rolled into a hollow cone covering the anthers and stigma. The anthers in most cleistogamous flowers are so situated that when the pollen is ripe and issues from the loculi it comes immediately into contact with the stigma. Sometimes, it is true, there is a tiny interval between the pollen adherent to the anther-lobes and the stigma, but in that case tubes are put forth by the pollen-cells in the direction of the stigma, and these tubes lay themselves upon the papillæ on the stigmatic surface and thence pursue their way to the ovules. In the cleistogamous flowers of the Henbit Dead-nettle (*Lamium amplexicaule*) it has even been observed that the anthers do not open, but that, nevertheless, pollen-tubes emerge from the pollen-cells, perforate the walls of the anther and grow in the direction of the stigma until they reach it. If a cleistogamous flower of this kind is examined after autogamy has been accomplished within it, one might at first sight think the anthers and stigmas were adnate to one another, so firm is the union of the pollen-tubes with the stigma.

As has been already said, all species of plants which produce cleistogamous flowers also develop other open ones. For the most part these latter possess very striking forms, scents, and colours, and are adapted to receive the visits of insects and to undergo cross-fertilization through their agency. It is interesting to note, however, that these open flowers possess none of the contrivances for effecting autogamy in the event of a dearth of insects. From these observations we are justified in supposing that we have here a sort of division of labour, inasmuch as the functions, usually discharged by one form of hermaphrodite flower alone, are here divided between two kinds of flower—both also hermaphrodite—viz., cross-fertilization is assigned to those that open, self-fertilization to those that remain closed.

Amongst Grasses, Rushes, Scirpuses, and other plants of the kind, which produce dust-like pollen in their hermaphrodite flowers, only a few species are known to possess cleistogamous flowers. The oldest established example is that of *Oryza*

clandestina, a widely-distributed bog-grass allied to the Rice-plant. The panicles of this *Oryza* include chiefly flowers which remain closed and are adapted to autogamy; they develop only on their very highest branches a few flowers which open and may be cross-pollinated by the agency of the wind. On the other hand, the number of species possessing cleistogamous flowers to be found amongst plants with adhesive pollen, and liable to be crossed by insect agency, is very large. Numbers of tropical and sub-tropical Aselepiadaceæ, Malpighiaceæ, Papilionaceæ, and Orchidaceæ afford instructive examples of this phenomenon. The splendid colours of the open flowers in these plants attract insects, and if the flowers are visited cross-pollination is rendered inevitable by the various kinds of apparatus for pressing, sprinkling, or shooting the pollen upon the insects with which the flowers are furnished; but if in spite of allurements no insects arrive, the stigmas are not besmeared with pollen at all, and these great open flowers wither without forming fruit. It then comes to the turn of the cleistogamous flowers. They are developed in the axils of special leaves as small, greenish, bud-like structures, which are destitute of means for alluring insects, but are none the less sure on this account to produce ripe fruit and fertile seeds. There is, besides, in temperate zones, no lack of plants in which the same phenomenon may be observed. A host of Bell-flowers, Rock-roses, Balsams, Polygalaceæ, Oxalidaceæ, and Scrophulariaceæ (e.g. *Campanula*, *Specularia*, *Helianthemum*, *Impatiens*, *Polygala*, *Oralis*, *Linaria*) and, in particular, the Violas of the *Nominium* and *Dischidium* sections, exhibit the same difference in the functions assigned to their two kinds of flowers. The beautiful *Viola mirabilis* has scented flowers stored with honey, which unfold great violet petals in the spring. If these blossoms are visited by hive- or humble-bees they are cross-fertilized; but many are not thus visited, and their fate is then to wither without effecting that process of autogamy which has been described (p. 387) as taking place in the species of Violet belonging to the *Melanium* section. In the summer, however, special branches of the same individual plant bring forth small green flower-buds which do not open, but nevertheless produce soon afterwards large ripe capsules full of seeds. This phenomenon, in apparent contradiction to the ordinary idea of the result of the flowering process, did not escape the attention of the Botanists of the eighteenth century, and they named this species of Violet, in which the majority of the large open blossoms fail to produce fruit whilst the closed bud-like flowers are invariably productive, *Viola mirabilis*, or the Wonderful Violet.

In *Viola mirabilis* and in all its allied species, called "caulescent" in the language of descriptive Botany, the cleistogamous flowers are developed on special shoots, and these shoots are either erect or else prostrate in long zigzags. This is also the case in several species of the Wood-sorrel genus (*Oralis*) and in *Arenaria agrimonoides*. A few Papilionaceæ (e.g. *Vicia amphicarpa*) and Cruciferae (e.g. *Cardamine chenopodiifolia*) are known too, whose cleistogamous flowers spring from underground runners or stalks, whilst the open flowers are borne upon aerial shoots. In several Violets of the kind called by descriptive Botanists "acaulescent", such as *Viola collina* and *V. sepium*, the cleistogamous flowers develop likewise

underground, their stalks springing from special shoots of the rootstock. In all these cases the two kinds of flowers are always borne on the same plant, though on different branch systems; there are, however, also instances, such as the Yellow Balsam (*Impatiens Noli-tangere*), where the open flowers are developed on different individuals from those which produce the closed ones. To be accurate we should say that the statement in each case expresses the general rule for the plants in question, for instances of transition are by no means uncommon. Thus, for example, individual plants of the Yellow Balsam do occur in which open flowers with large corollas, half-open flowers with stunted corollas, and small cleistogamous flowers stand side by side; and, again, on the zigzag runners of the Sand Violet (*Viola arenaria*) flowers with large expanded petals have often been seen growing in company with the cleistogamous flowers. The same remark applies as regards the time at which cleistogamous flowers make their appearance. In the majority of cases they are not developed until the open flowers have withered and disappeared, but in *Cardamine chenopodiifolia* it has been observed that the subterranean cleistogamous flowers are produced earlier than those which are borne on above-ground stems and unfold their petals to the air.

In former times it was asserted that plants exist which never bear any but cleistogamous flowers. Thus the Toad-rush (*Juncus bufonius*) was stated to produce cleistogamous flowers only. Later investigations have, however, established the fact that this plant possesses two kinds of flowers—viz. terminal flowers with three stamens which are cleistogamous, and lateral flowers with six stamens which open, like those of other Rushes, under the warmth of the noonday sun. It was also supposed that the African species of *Salvia*, to which the name of *Salvia cleistogama* was given, produced cleistogamous flowers only, but after repeated sowings plants have been obtained with flowers which opened. Anyone who has only seen the Yellow Balsam growing on the heaps of detritus brought down by the mountain-streams in the upland valleys of the Tyrol might think that this plant also was an instance of a species producing cleistogamous flowers only; for in those localities open flowers are not found on this species. But if seeds from these cleistogamous flowers are sown in good vegetable mould, in a partially shaded spot in a garden, a few individuals with large open yellow flowers spring up, as a general rule, even after a single sowing. There is a species of Violet named *Viola sepincola* which grows deep in the shade of the woods clothing the hills at the foot of the Solstein chain in the Innthal district. I saw it there for the first time about the middle of May, and it was then covered with an abundance of ripe fruit. In following years I looked for flowers of this plant early in the spring, as soon as the snow had melted, but found that not a single individual had developed open flowers with expanded petals on erect above-ground stalks. On the other hand, there were a number of cleistogamous flowers concealed under the fallen leaves and partially buried in the earth, so that it looked very much as if the species produced no other kind of blossom. But plants subsequently reared in a part of my garden which was exposed to the sun's rays during some hours of each day developed, in the next

year but one after their being sown, in addition to cleistogamous flowers, beautiful scented blossoms of a violet colour which were borne on erect stalks and in due time unfolded their petals.

This result throws some light on the nature of the stimulus which causes the formation of the flowers in question. No open, aerial flowers were produced by *Viola sepincola* so long as it grew in the cool shade of a dense wood, but when transferred to open ground, accessible to sunlight, such flowers were developed. One can hardly err in ascribing to the sun's rays a very important influence in stimulating plants to the inception of flowering shoots, especially such as bear blossoms possessing bright-coloured petals. Indirectly, however, this advantage accrues to the plants in question that, living as they do in the deep shade, where no bees would, in any case, visit them, even if they had open flowers, they can confine their constructive energy to the inception and development of cleistogamous flowers and save themselves the trouble of producing open flowers adapted to cross-pollination (but useless in the place in question). If the spot where the Violet grows becomes exposed to the sunlight through the trees shading it being blown down or felled, humble- and hive-bees make their appearance in search of honey, and, buzzing from flower to flower, cross one with another. In such circumstances the open, sweet-scented Violet blossoms are in request, and the same plant-individual, which for years in the dark shade has developed none but cleistogamous flowers, is now stimulated by the sun's rays into producing flowers with expanded petals.

A similar instance is afforded by the Henbit Dead-nettle (*Lamium amplexicaule*), which grows on cultivated ground—in kitchen-gardens, vineyards, and amongst crops. This plant bears two kinds of flowers, viz. some with purple corollas 15 mm. in length, which keep the entrance leading to their honey wide open, and, secondly, cleistogamous flowers with abortive corollas and small green calices, which remain closed. As is the case with many other annual weeds, Dead-nettle plants which have germinated late in the season maintain their vitality through the winter and into the following spring, and accordingly they may be seen at all seasons flourishing, fresh and green, in situations such as are mentioned above. Flowers, too, are initiated and developed by them at all seasons of the year, but it is interesting to note that only in the warm summer, when flower-seeking insects are about, are the beautiful purple corollas of this plant to be seen; in the late autumn and early spring, when it is cool, and there are no flower-seeking insects, this Dead-nettle is able to do without the luxury of corollas, which are the means of alluring insects, and as a fact only cleistogamous flowers make their appearance at those seasons. It must not, of course, be imagined that the plant exercises an intelligent discretion of its own when it abandons the development of corollas. The connection between this effect and the aforesaid conditions is indirect, and we must conceive that the nature of the stimulus which results in the inception of flower-buds is different, when a plant is subject to the influence of the short days and low temperature of late autumn and early spring, from what it is under the conditions prevailing on warm summer days.

Amongst the contrivances mentioned in the last chapter as being adapted to bring about cross-fertilization at the commencement of a flower's period of bloom, was the production of heterostyled flowers (see pp. 302 and 312). It was pointed out (p. 316) that in heterostyled plants the very first, or last (as the case may be), of all the flowers of a particular species are, in consequence of the dichogamy which prevails, fated to be crossed with flowers of another species, or, in other words, to undergo hybridization, and that, according to experience, this crossing is often effective. Considering the results obtained in the cases of other plants with hermaphrodite flowers, one would expect to meet with some provision for the timely fulfilment of autogamy in heterostyled species as well, *i.e.* that in the event of no insects visiting a plant of the kind, the stigmas should at the proper moment be dusted with pollen from the anthers in the same flower. This expectation has been, in fact, confirmed; all the investigations directed to this question having resulted in showing that a process of autogamy takes place also in heterostyled flowers, but is always confined to one only of the forms which together constitute the species. In one section of the heterostyled species, including, for example, those which belong to the genera *Gentiana*, *Menyanthes*, and *Thesium*, the short-styled flowers are adapted to autogamy, whilst in others, such as the heterostyled species of *Mertensia* and *Pulmonaria*, autogamy takes place in the long-styled flowers. In *Primula longiflora* and *P. minima* it is the short-styled flowers which have their stigmas dusted with pollen from their own anthers, whilst in *Primula Auricula*, and *P. glutinosa* it is the long-styled flowers which thus accomplish self-fertilization. All these variations are exactly adjusted with reference to the other arrangements for promoting autogamy in the flowers in which they are exhibited.

One contrivance which deserves mention here is the disparity in the size and conspicuousness of the floral envelopes in the two forms of flowers of the same species. In *Primula longiflora* and *P. minima* the long-styled flowers, and in *Primula Auricula* and *P. glutinosa* the short-styled flowers have a larger and more striking limb to their corollas than the other forms in each case. It may be taken to be a general rule that the flowers adapted to cross-fertilization, in which no autogamy takes place, are larger than those in which the accomplishment of autogamy is assured. This phenomenon has been explained by the circumstance that flowers destined to be crossed with others require to be more plentifully equipped with the means of attracting insects than those which are certain to undergo fertilization even if no insects visit them.

The means whereby autogamy is achieved in species with heterostyled flowers are in the main the same as they are where the flowers are not heterostyled. In some cases the stamens, or the petals with pollen affixed to their surfaces, elongate sufficiently to enable the stigmas to come into contact with them: in others the same result is attained by an inclination or an inflection of filaments or style; in a third series the stigma is dragged through the ring of anthers when the corolla falls off, or the petals by opening and closing effect the transference of the pollen from the anthers to the stigma; and lastly, in some instances, the pedicels undergo elongation

and inflection, which result in bringing the stigma underneath the anthers, so that when the latter shrivel their pollen must fall upon the receptive tissue. Of the host of observations relating to this matter, we can here only select a few to serve as examples, and the most suitable for our purpose will be the *Primulas*, to which reference has already been frequently made, viz. *Primula Auricula*, *P. glutinosa*, *P. longiflora*, and *P. minima*.

The corolla in the short-styled flowers of *Primula Auricula* has a comparatively large expanded limb, the surface of which is slightly concave; the five stamens are adnate to the contracted throat of the corolla, where the tube passes into the limb, and the anthers form, at that part of the flower, a ring through the middle of which insects must penetrate in order to enter the floral interior. The style is short, and the spherical stigma at the top of it stands at a level corresponding to only a third of the length of the corolla-tube. At the time when the dehiscence of the anthers takes place, the flowers are in a nodding or horizontal position. In these circumstances no pollen can reach the stigma, and, unless visited by insects, the flower remains unpollinated until it fades, nor does the fall of the corolla operate as a means of conveying pollen from its own anthers to the receptive tissue. It is quite different with the long-styled flowers of the species in question. The limb of the corolla is rather smaller, and is hollowed into the shape of a basin; the five stamens are adnate to the lowest third of the tube, and their anthers stand at the same height as does the stigma in a short-styled flower. The style is long, and the stigma may be seen in the middle of the flower's throat. In other respects there is no difference worth mentioning between the two forms. The stigmas of the long-styled flowers are liable to be dusted with pollen brought by insects from the anthers stationed in the throats of short-styled flowers. Whether this occurs or not, the receptive tissue under any circumstances gets covered with pollen when the corolla becomes detached and falls off, for the stigma is then dragged through the ring of anthers in the corolla-tube, and is certain to remove some of the pollen which still adheres in more or less abundance to them.

Altogether different is the process of autogamy as manifested in *Primula longiflora*. In this case the corolla of a long-styled flower has a shorter tube and larger limb than that of a short-styled flower. The anthers are situated in the throat just behind the mouth of the corolla-tube. The style is long and projects far beyond the throat, whilst the stigma is held considerably above, that is to say, in front of the ring of anthers. The flowers are either horizontal or else ascend obliquely, and neither of these positions admits of pollen being deposited by the anthers upon the stigma. As in this species the corolla does not drop but persists even when withered no autogamy takes place in the long-styled flowers when the plant is growing wild. On the other hand, every insect which enters the flower must necessarily touch the stigma, stationed where it is in front of the passage, and cross-fertilization then ensues. The short-styled flowers have a longer tube and smaller limb to the corolla. Their anthers, unlike those of many other *Primulas*, are situated in the throat close beneath the corolla-limb in the same position as in the long-styled flowers; but the

style does not project outside the throat, and its stigma rests only just above the tips of the anthers. Under these conditions cross-pollination is as likely to be brought about through insect-agency as it is in the case of the long-styled flowers; but in addition autogamy takes place towards the end of the period of bloom. The manner in which the latter is effected is as follows:—During the period of the flower's bloom the corolla-tube grows some millimetres in length until finally the ring of anthers, which are adnate to the throat of the corolla, is brought up to the same level as the stigma. The stigma then stands in the centre of the ring and receives an abundant supply of pollen from the adjacent anthers.

In *Primula minima* (see figs. 288¹ and 288², p. 302) the heterostyled flowers are erect and maintain this position unaltered till the corolla withers. The limb of the corolla in the long-styled form (see fig. 288¹) is larger than it is in the short-styled form. The anthers in the long-styled flower are inserted on the lower part of the tube; the style projects above the ring of anthers and the stigma rests somewhere in the uppermost third of the tube. On entering a flower an insect would first come against the stigma, and would then probably dust it with foreign pollen. Autogamy scarcely ever takes place. In the wild state of the plant the corolla withers without falling off; only in rare instances does it happen that the corolla becomes detached from the receptacle, and is carried away by the wind. On such an occasion the stigma might touch the ring of anthers and get covered with pollen. Self-fertilization is, on the other hand, all the more carefully ensured in the short-styled flowers. Here the anthers are attached to the highest third of the corolla-tube, and the stigma capping the short style rests below the ring of anthers. When the flower's period of bloom is nearly at an end both the corolla-tube and the anthers begin to wither and contract, with the result that the pollen falls from the anthers down the tube, and is caught upon the stigma.

Thus, autogamy is effected in the long-styled flowers of *Primula Auricula* and *P. glutinosa* by the stigma being dragged through the ring of anthers as the corolla falls off, in the short-styled flowers of *Primula longiflora* by the elongation of the corolla-tube and elevation of the anthers to the level of the stigma, and in the short-styled flowers of *Primula minima* by the anthers shrivelling and letting their pollen fall. The fact of the occurrence amongst Primulas alone of three kinds of contrivance for promoting autogamy gives us some idea of the immense variety which prevails in this respect amongst heterostyled plants in general. The impossibility of entering here into the further details of this subject is the less to be regretted, seeing that to a great extent such an account would involve a repetition of facts which have already been stated.

The number of species possessing heterostyled flowers is far larger than was formerly supposed. The list of such species known at the present day includes members of the following families: Boraginaceæ, Caprifoliaceæ, Caryophyllaceæ, Colehicaceæ, Crassulaceæ, Ericaceæ, Gentianaceæ, Globulariaceæ, Iridaceæ, Linaceæ, Lythraceæ, Onagraceæ, Oxalidaceæ, Papaveraceæ, Plantaginaceæ, Plumbaginaceæ, Polygonaceæ, Primulaceæ, Rubiaceæ, Santalaceæ, Solanaceæ, and Valerianaceæ, and

it is probable that more thorough investigation will result in the addition of many more instances, especially amongst tropical plants. In most cases the species of one genus produce only two forms of flowers; but there are also genera—such as *Linum* and *Oxalis*—in which some of the species develop long-, mid-, and short-styled flowers, others long- and short-styled forms, and others again none but flowers with styles of equal length. The determination of the point as to whether heterostylism exists or not in a particular case is, in many species, attended with some difficulty, owing to the stamen-filaments increasing in length during the period of the flower's bloom in both the long-styled and the short-styled flowers—a circumstance which greatly complicates the relations subsisting between the two forms in respect of the lengths of their different parts. There is also some danger of mistaking for heterostyled species a class of forms which do not in reality come under that category. In the species alluded to, a proportion of the individual plants produce apparently hermaphrodite flowers, with ovaries, styles, and stigmas which can be clearly identified as such, but which nevertheless are not capable of undergoing fertilization.

The results of the investigations into the subject of autogamy recorded in this chapter may be summed up as follows. In plants whose flowers are hermaphrodite, but neither cleistogamous nor heterostyled, both cross- and self-fertilization occur in one and the same flower at different epochs; in plants with cleistogamous flowers a division of labour is established between two kinds of hermaphrodite flowers, of which the one form opens and is adapted to heterogamy, whilst the other remains closed and can only result in autogamy; and, lastly, in heterostyled plants, each species includes two or three different forms of individual, varying in respect of the structure of the flowers, which in the one case aim at cross-fertilization, and in another especially at autogamy.

In view of the detailed consideration which the methods for promoting autogamy in various plants has received in the foregoing pages, it may not be without interest to allude here briefly to the relative prevalence of this mode of pollination in certain Floras. During the passage of the present edition of this work through the press, a notable addition to our knowledge of Floral Biology has been made by E. Loew (*Blütenbiologische Floristik*), in the form of a treatise wherein are summarized the vast number of observations upon flowers and their relations to insects, &c., so far as the Floras of Europe and Greenland are concerned, that have been published in one place and another during the last ten years. This tabulating of observations has enabled the author to make many interesting comparisons between the Floras of various regions, and, supported by statistics, to exhibit the relative prevalence of types adapted to this or that method of pollination. Though many of the results do but confirm views already the common property of Biologists, they have an altogether special value from the manner in which they have been obtained.

As regards autogamy, it appears from statistics that it shows an increase in high Alpine forms as compared with plants from a lower level. The accompanying

table, taken from Loew, contrasts alpine and sub-alpine plants in regard to the relative prevalence of autogamy:—

- (I.) Of 130 entomophilous plants in *sub-alpine* regions—
 35 species = 26·9% are rarely or never autogamous.
 86 species = 66·1% are autogamous as well as heterogamous.
 9 species = 6·9% are invariably or usually autogamous.

 99·9%
- (II.) Of 133 entomophilous plants in *high alpine* regions—
 35 species = 26·3% are rarely or never autogamous.
 78 species = 58·6% are autogamous as well as heterogamous.
 20 species = 15·0% are invariably or usually autogamous.

 99·9%

Thus we see that 20 high alpine species show pronounced autogamy as compared with 9 sub-alpine forms.

In the mountain Flora of Scandinavia the prevalence of autogamy is even more marked.

- (III.) Of 74 species from the Dovrefjeld—
 12 species = 16·2% are rarely or never autogamous.
 40 species = 54·0% are autogamous as well as heterogamous.
 22 species = 29·7% are usually autogamous.

 99·9%

As compared with the high alpine plants (table II.) we note a diminution of 10% in those which are always heterogamous, and an increase in those usually autogamous of some 15%.

In plants whose distribution is restricted to the Arctic regions, the number of autogamous plants is in the majority.

- (IV.) Of 45 species of purely Arctic plants—
 0 species = 0·0% are almost exclusively heterogamous.
 14 species = 31·1% are autogamous as well as heterogamous.
 26 species = 57·8% are usually autogamous.
 5 species = 11·1% are doubtful.

 100%

Precisely what factors in their environment have led to this increased prevalence of autogamy in high alpine and far northern species is at present not certainly determined. A lack or comparative rarity of insect-visitors on the one hand, or unfavourable climatic conditions on the other, might either of them well lead to such a condition. Regarding the alleged paucity of insects in the Alps, one so well qualified to speak as Hermann Müller says¹:—"I have not been able to convince myself that alpine flowers are, on the whole, less frequently visited and crossed by insects than are those of the plain". Nor does Loew, with the statistics before him, dissent from Müller's opinion. So also with regard to the northern types, concerning which the view is widely spread that their preponderating autogamy is connected

¹ *Alpenblumen*, p. 547

with the paucity of insects. Loew is of the opinion that the insects there are adequate for the work they have to do, *i.e.* are sufficiently numerous for the maintenance of the species of plants which depend upon their visits.

Putting aside the visits, and proceeding to consider the climatic conditions, we are on much surer ground. Both on the mountains and in the far north the period of vegetation is a short one, and the shortness of the summer, combined with the broken character of the weather, which is common to the Alps and Arctic regions during that period, can hardly fail to promote autogamy amongst the plants growing in those regions. Such as have flowers that can pollinate themselves spontaneously will be more sure of ripening their seeds before the brief summer ends than will such the flowers of which must wait for insects. In the foregoing pages several instances have been described in which autogamy is promoted by the closing of the flowers. By these movements the pollen is mechanically transferred to the stigmas. It may well be that by the considerable increase which must accrue in these closing movements, owing to the frequency of unfavourable weather in alpine and arctic regions, a further condition favouring autogamy is obtained.

FERTILIZATION AND FORMATION OF FRUIT IN PHANEROGAMS.

Pollination, or the dusting of the stigma with pollen, is only the prelude to the phenomenon known as *Fertilization*. It is important to distinguish clearly between these two events, especially as the term "fertilization" is frequently used by authors when they really mean "pollination"—indeed, this substitution is almost inevitable in many cases, the custom being what it is. Fertilization can only occur in Phanerogams after previous pollination, though pollination does not invariably connote a subsequent fertilization. Thus, cases are known in which flowers, pollinated by insects at the proper time, do not produce fruit, and others in which the pollen of the same flower falls upon the stigmas with a like failure of result. In other words, both cross-pollination and autogamy may be without result.

It must be explained, to prevent misunderstanding, that the older accounts of this lack of result attending pollination should be received with caution. Formerly, judgment was passed rather hastily as to the results of pollination in hermaphrodite flowers, as it seemed obvious that the sexual elements must, unavoidably, come together. If no production of fruit took place in a really hermaphrodite flower, it was assumed that pollination was without result, and no precautions were taken to demonstrate that pollination had actually occurred. Thus it happened that certain plants were regarded as sterile, although this sterility had only been observed upon isolated specimens growing in gardens. In many cases the flowers of the plants in question were strongly protogynous, *i.e.* at the time when the stigmas should have been pollinated there was no pollen, there being no plants growing near with flowers in a more advanced stage. Similarly, such flowers cannot be autogamous, as the two sets of organs are never at maturity simultaneously. They are marked out for cross-pollination. When for any reason this does not take place, fertilization

and fruiting obviously cannot occur. It is instances of this kind that are adduced by the older botanical writers to prove that the hermaphrodite flowers of certain species are infertile.

Plants have also been regarded as sterile from the fact that the particular insects necessary for the transfer of their pollen were absent from the locality in which the observations were made. Thus, *Paederota Algeria*, a plant not infrequently found in rocky crannies in the Southern Alps, and cultivated in large quantity in the Innsbruck Botanic Garden, was always found to be sterile in the last-mentioned locality, although it flowered profusely. The flowers of the plant require insects to pollinate them, as the relations of the parts are such that autogamy cannot occur. Since the particular insects which visit it in its own habitat are absent from the Botanic Garden, the plant is infertile from lack of pollination. In its own home in the Southern Tyrol and Krain, where these insects are present, it ripens an abundance of fruits. The same is the case with several introduced plants which have become partially wild. The Sweet Flag (*Acorus Calamus*), truly indigenous to Eastern Asia, has spadices of densely-crowded, hermaphrodite flowers. The individual flowers are strongly protogynous, and when the anthers open, the stigmas of the same flower are already faded. Autogamy is consequently excluded. The opening of the flowers is from below upwards, and when the anthers of the lowest flowers are discharging their pollen the stigmas of the uppermost flowers are still capable of pollination. Could the pollen pass from the lower to the upper flowers, geitonogamy would take place, but this is only possible through the agency of insects, as the pollen is adhesive. In Europe, where the plant is not originally indigenous, this never happens, as the insects which visit it are absent; consequently, with us, *Acorus* is always sterile. But further east, where it is indigenous, its flowers are pollinated by insects, and it produces its fruit in spikes of red berries. The Day Lily (*Hemerocallis fulva*) has ephemeral flowers which open in the morning in summer-time between 6 and 7 o'clock, and close between 8 and 9 in the evening. Its flowers are protogynous for a very short time. For half an hour before the opening of the flower the mature stigma projects from the tip of the perianth. Simultaneously with the folding back of the perianth, the anthers liberate their adhesive pollen. The style being longer than the stamens, its stigma is not automatically pollinated. For pollination insect visits are necessary. Honey is secreted at the base of the tube of the perianth, which is 2 cm. long. The entrance to this honey is so narrow that only a very delicate proboscis can gain access. Beetles, flies, bees, and other short-tongued insects cannot get it, nor would they be of any use for pollination if they could. The whole flower seems adapted for the visits of some large butterfly with a long, thin proboscis, but curiously enough the flowers of *Hemerocallis fulva* are never visited by butterflies in Europe. As autogamy is excluded, the flowers remain unpollinated, and are sterile. Neither in gardens, where it is much cultivated, nor in its semi-wild state does the Day Lily ever fruit with us. It is more than probable that *Hemerocallis* is visited, in Northern Asia and Japan, where it is truly indigenous, by some butterfly absent from Europe.

It has been already mentioned (p. 156) that the flowers of the American Yuccas are pollinated by small moths, unknown in Europe, and that these flowers set no fruit with us. Also, that several species of Catchfly, indigenous to the Southern and Eastern Alps, though robbed of their honey by humble-bees, are but seldom pollinated and fruitful (p. 239).

Lastly, many cultivated plants, depending on insects for fertilization, flower in gardens earlier or later than in their wild surroundings. In nature, their period of flowering coincides with the time of flying of certain insects; in gardens—even when the insects in question occur—the flowers may be too early or too late for the insect season. From what has been said above, it will appear that sterility in many cases is only apparent, and is due merely to the lack of the normal and necessary conditions for bringing about pollination.

In other cases it may happen that although the stigmas are pollinated, the pollen cells are abortive and incapable of producing pollen-tubes. This condition of the pollen obtains most frequently in gardens amongst plants on rich, well-manured soil, artificially-produced hybrids, and plants whose stamens are partly converted into petals. At the same time it must not be supposed that by any means all plants which show a “doubling” produce bad pollen; for instance, many double Roses produce pollen which is used by gardeners for artificial pollination with good results. Still, in the majority of such plants abortive pollen is the rule, pollen which is non-effective on the stigma.

In nature, especially in places where many plants flower at the same time, as on the borders of a wood, in meadows and heaths, it is unavoidable that the pollen of various species should be deposited on one and the same stigma. Insects certainly show a preference for a single species for considerable periods, particularly when this species is flowering in quantity on a confined space: still, anyone who closely observes insects visiting flowers can easily convince himself that the flowers visited are changed from time to time. A bee which has just dusted itself with pollen in the flower of a Winter Aconite (*Eranthis*) will fly across to visit a bush of *Salix daphnoides*, and as it passes a plant of *Daphne Mezereum* it will suck its honey; a moment later it will swoop down to the flowers of *Crocus vernus* in the meadow near by, and then fly on to the Sweet Violet (*Viola odorata*). On the stigma of the last-mentioned plant will be found the pollen of all or several of the just-visited flowers, on the Crocus that of the Willow, and so on. The case is similar with wind-pollinated flowers. I have found the pollen of the Spruce Fir (*Abies excelsa*) and of Dog's Mercury (*Mercurialis perennis*), both brought by the wind on to the stigmas of the Herb Paris (*Paris quadrifolia*); and on another occasion the stigmas of *Gagea lutea* were so thickly dusted with the pollen of *Alnus viridis* that there would have been no room for any pollen more.

That the pollen of the Willow will fertilize the Crocus, that of Dog's Mercury the Herb Paris, or that of the Alder the Gagea is *a priori* improbable. Only such changes take place in the pollen as always occur when it is placed on a moist substratum: all further stages in its development are arrested. The commencing

pollen-tubes, sometimes found, though in some cases they penetrate the tissues of the stigma, do not fertilize the ovules. It is another question whether or no this "foreign" pollen is entirely without effect, whether it does not possibly influence the stigmatic tissue so that less foreign pollen, arriving later on the same stigma and developing pollen-tubes, is affected. But this subject can only be dealt with later on; here it suffices to state that all pollen falling on a stigma is not necessarily suitable, and that the stigma has, in a manner of speaking, to make a selection.

It is very difficult to say what conditions come into play in this choice of pollen. Experimental inquiry into this matter has not been wanting, but its results tell us little as to the fundamental processes at work. By it we ascertain little more than whether this or that artificial pollination leads to a production of seeds or not. Thus in one case no seed will be formed, in another a few, and in a third case an abundant crop. The sources of error in this class of experiment are considerable, nor do the results by any means always harmonize. Thus, in experiments of my own as to the fertility of certain *Catchflies* when pollinated from allied forms, no result would be obtained in one year, whilst in the following year their repetition led to the production of a certain number of seeds. Other observers have had the same experience; and it would seem that whatever care be exercised, absolute reliance cannot be placed on the result—especially where it is a negative one. Caution must be used, therefore, in generalizing from such experiments, especially in cases where their number is limited. In the main, the general results are very instructive, and must not remain unnoticed here in so far as they relate to the connection between fertilization and the origin of new species.

These results may be shortly summarized as follows. When the pollen of one species is placed on the stigma of another species, pollen-tubes capable of fertilizing the ovules are developed only when the two species belong to the same genus or to the same natural family of plants. Families and genera are conceptions devised by Botanists, and although their limitations are to some extent arbitrary or dependent on the personal equation of individual observers, in the main there is little difference of opinion as to these limitations in the case, at any rate, of families. How far new discoveries may lead to a revision of their present limits must remain undecided, but, of families as at present laid down, we may say that crossings of pollen between species of two different families (orders) is without result, whilst between species of two different genera very rarely is seed produced.

The crossing of species of the same genus results, in most cases, in fertilization, and eventually in the production of hybrids. It is certainly remarkable, in this connection, that external similarity between the two species crossed has little bearing on the result or absence of result. One of the commonest of naturally-produced hybrids is one which owes its origin to the union of *Primula glutinosa* with *Primula minima*, two species very dissimilar in the form of their foliage and flowers. On the other hand, hybrids of the very similar Cowslip and Bardfield Oxlip (*Primula officinalis* [*veris*] and *Primula elatior*) are but rarely met with in nature, whilst artificial pollinations between them only occasionally lead to any result.

If ripe pollen from the male flowers of a plant be placed on the mature stigmas of female flowers of the same species, the result may be regarded as certain. This holds good equally for monœcious and diœcious plants, and for such also as have apparently hermaphrodite flowers in which one or other set of sexual organs is more or less abortive, so that the flowers in question are to all intents and purposes unisexual.

It has been shown that for plants with true, non-heterostyled, hermaphrodite flowers, a transfer of ripe pollen from the anthers of one flower to the mature stigma of another, belonging to the same species, constantly leads to fertilization. In those cases only in which the stamens are of unequal lengths is pollination attended with unequal results, according as the pollen has been taken from the longer or shorter stamens.

The behaviour of plants with hermaphrodite heterostyled flowers is peculiar. Pollen from the anthers of a short-styled flower applied to the stigma of a long-styled flower, or from a long-styled flower applied to the stigma of a short-styled flower, gives the best result. The other possible combinations, *i.e.* pollen from long-styled or short-styled flowers applied to the stigmas of the same class of flower give indifferent results, and frequently none at all. Experiments have shown in the case of the Loosestrife (*Lythrum Salicaria*), which, as we have seen (p. 303), possesses long-, mid-, and short-styled flowers, that crossings between stamens and styles of the *same* length ("legitimate unions") are fruitful, whilst all other crossings ("illegitimate unions") are either quite sterile or followed by only a sparing production of seed.

It has been demonstrated that the pollen-cells of heterostyled flowers vary both in size and colour according to the length of stamen (or height of anther or corolla) producing them. Thus, in the Loosestrife, the dry pollen-cells of the long stamens are green, and $30-38\ \mu$ long and $20-26\ \mu$ broad; those of stamens of the middle length are yellow and $23-26\ \mu$ long and $13-16\ \mu$ broad; those of the short stamens are also yellow, but $20-25\ \mu$ long and $11-13\ \mu$ broad ($\mu = \frac{1}{1000}$ millimetre). In the Cowslip (*Primula officinalis* [= *veris*]) the pollen-cells, produced by anthers at the mouth of the corolla-tube (and destined for a long style), have a diameter of $30\ \mu$, those arising from anthers low down the tube (and destined for a short style), a diameter of only $20\ \mu$. The explanation offered by Delpino of this difference in size—that, other things being equal, pollen-tubes which have to traverse a greater distance to reach the ovules require a more ample supply of reserve-materials than those which have less far to penetrate—sounds plausible, but the problem is probably a rather more complex one than appears at first sight. As a general result of experiments upon heterostyled plants we may say that the most copious production of good seed results from a pollination of stigmas with pollen from stamens of similar height.

As to the result of *autogamy* (self-pollination) in ordinary hermaphrodite flowers, it would appear, in all cases where the stamens are of unequal heights, that the pollen has a dissimilar effect according as it comes from a longer or shorter stamen. If pollen, which *would not unaided reach the stigma* of the same flower, be artificially transferred to that stigma, the product is usually very small. If, however, *pollen which would ultimately reach the stigma* of the same flower be artificially

transferred thither a good crop of seed results. Artificially produced autogamy in hermaphrodite flowers, in which the stamens are all of one length, is generally productive, nor does it appear to matter whether the pollen used for pollination be taken from the first stamen to open or the last. The number of species in which artificial autogamy is unfruitful is extremely small. *Crambe tatarica*, *Draba repens*, *Lilium bulbiferum*, *Lysimachia nummularia*, and a few Orchids and Papilionaceæ may serve as examples, though even in these cases it is quite possible that some source of error, such as was mentioned at the commencement of this chapter, has been overlooked.

We may now proceed to discuss what is known as the *prepotency of foreign pollen over own pollen*. The term "foreign" is used of pollen upon a stigma which has been brought from another flower of the same or of some other species; "own" pollen, on the other hand, is applied to such as has originated in one of the anthers of the *same* flower. These terms are employed for the sake of brevity. If one examines a flower of *Corydalis* early in the morning of the day on which that flower will become accessible to insects, one finds that the anthers have already dehisced, and that the stigma is covered with own pollen. The stigma, lying between the two spoon-shaped petals, is regularly embedded in pollen. But as yet the stigma is immature and unreceptive, so that the absence of any interaction between pollen and stigma at this stage is intelligible. When insects come in due course, a portion of this pollen will be removed (*cf.* p. 266). Should the insects have visited *Corydalis*-flowers previously, they will leave some of the foreign pollen with which they are dusted upon the stigma at the moment when they remove some of the own pollen. The stigma is now in contact with both own and foreign pollen, nor will additional insect-visits materially alter this state of affairs. In due time the stigma becomes receptive and exerts a selective action upon the pollen. Though the process, as it takes place here, cannot be followed step by step, still we are justified in assuming, on the results of many experiments of artificial pollination, that the foreign pollen receives the preference. It has been shown for *Corydalis cava* that the flowers are absolutely barren to their own pollen, only slightly fertile to pollen from another flower on the same plant, and only thoroughly fertile when impregnated with pollen from a different plant. For other species, however, e.g. *Corydalis capnoides*, *fabacea*, and *ochroleuca*, it has been shown that the plants are fertile to their own pollen, so that if no insect-visitors come, the flowers do not remain sterile.

These results show how fallacious it would be to make the condition obtaining in *Corydalis cava* the basis of any far-reaching generalization, such as that autogamy is prevented, and without result. In point of fact, autogamy is highly productive in most species of *Corydalis*, and occurs, in such plants as are unvisited by insects, in the closed flower in a manner recalling that form of autogamy known as cleistogamy (*cf.* p. 391). That foreign pollen is prepotent in *Corydalis capnoides*, *fabacea*, *ochroleuca*, &c., when both foreign and own pollen are present on the stigma together, is neither asserted nor denied, though, in view of all the circumstances, it seems probable.

In agreement with *Corydalis* stand numerous species of *Fumaria*, and a great number of Papilionaceae, especially those whose flowers possess a piston apparatus (cf. p. 260). *Pisum* and *Ervum*, *Lotus* and *Melilotus*, the various species of *Trifolium*, almost all of them, when unvisited by insects, ripen seed, only a few species here and there being infertile when dependent upon their own resources. Thus we may say that when the stigma has to choose between own and foreign pollen, the latter probably gets the preference, though, when own pollen alone is present, it is adequate for fertility.

A similar condition obtains amongst the Scabiouses (*Scabiosa*) also. Their flowers are hermaphrodite and protandrous, and united into heads. At the time when the anthers dehisce, the pollen remains hanging to the stigmas, although these are not as yet actually receptive. For the time being, this pollen is without effect. By the visits of insects a portion of this pollen is removed and replaced by foreign pollen, which is ultimately, on the maturing of the stigmas, probably preferred to the own pollen. In the absence of insects, however, the flowers are undoubtedly fertile to their own pollen.

Likewise, in many Labiates (e.g. *Leonurus heterophyllus*) and Scrophulariaceae (e.g. *Linaria littoralis* and *minor*), has essentially the same state of affairs been shown to exist. One more instance only need be described, that of a Catchfly (*Silene noctiflora*). This plant opens its flowers at about seven in the evening. If, however, the flowers be opened artificially a little earlier, at about six p.m., it is found that all the anthers have already dehisced, and that the delicate stigmatic papillae are already dusted with the pollen from the five short stamens. Thus, already in the bud, autogamy has taken place in a manner not unlike cleistogamy. As the flowers open in spite of this, it can only be on the chance of crepuscular or nocturnal moths visiting them and bringing foreign pollen. The flowers of this Catchfly are not very eagerly sought after by insects, still now and again a *Plusia* or other owlet moth may be seen flitting from flower to flower, sucking honey and bringing and taking pollen. Thus, again, a selection of pollen by the stigma probably occurs with preference for the foreign; otherwise, why need these flowers open at all since the stigmas are already coated in the bud with own pollen? In the absence of insects the own pollen will be potent and lead to seed-production. In wet, cold weather also, when the flowers do not open at all, the ovules ripen into seeds, no doubt impregnated by their own pollen. In all the cases enumerated the behaviour is essentially the same, in the early stages of flowering the opportunity is given for cross-pollination by insects, but, wanting this, autogamy or self-pollination ensues.

We may now pass on to speak of the *germination of the pollen-grain* upon the stigma and of the development of the pollen-tube. The pollen is at this stage influenced by the receptive stigma. There would appear to be a taking up of fluid matter by the grain, though its exact nature has not been accurately determined. Since, however, pollen-grains germinate readily in a 3-per-cent sugar-solution, it is extremely probable that sugar is an important component of this stigmatic fluid.

The first demonstrable stage in the production of the pollen-tube is the pushing

out of the delicate inner coat of the grain in the form of a tube through the thin places in the extine. The structure and distribution of these thin spots has been already described (p. 102); it need only be added that a tube may be pushed out at each or any of them. When pollen is artificially cultivated in a prepared sugar-solution several tubes arise simultaneously from different spots, but, in nature, on the stigma, the production of a single tube is the rule. The tube which contains the whole of the contents of the pollen-grain (spermatoplasm) forsakes the extine, which remains behind as a dead shell. Very soon after its appearance through one of these holes in the extine, the pollen-tube comes to have a considerable diameter, often approaching that of the grain in size. The tube now elongates, growing always at the expense of the stigma. Its mode of growth is similar to that of a fungal hypha, and its relation to the stigmatic tissues resembles that of the hypha of a parasitic fungus to its host. Like the parasite, it is able to penetrate the subjacent tissue and to make its way through it for long distances.

This penetration by the pollen-tube is certainly amongst the most remarkable properties of flowering plants. The object of these wanderings is to reach and fertilize the ovules contained—in Angiosperms—in the closed chamber of the ovary. Whether the stigma be sessile upon the ovary or situated upon a style, the distance to be traversed is considerable, and, in a very large number of cases, the way leads through closed tissues. As the pollen-tubes travel as a rule by definite rows of cells or tracks, we may assume that these latter are in some way specialized for their conduction; still it is very puzzling to understand exactly in what manner these cells become thus qualified. In all likelihood the pollen-tubes are attracted by certain substances secreted by the tissues, which they have to traverse in order to reach the ovules. Of these sugar seems to be the most important, and by a continuous secretion of this (and possibly other substances), the tubes are led on to the ovules. Casual allusion has already been made to the fact that the motile spermatozoids of Cryptogams swim through the water to the archegonia (amphigonia) in response to a somewhat similar stimulus (p. 68).

Investigations into the course followed by the pollen-tubes in passing from the stigma to the ovules show that it varies in different cases. Simplest, and perhaps typical of what was formerly supposed to be the route universally followed, is the case of the Martagon Lily (*Lilium Martagon*, cf. fig. 313¹). If the columnar style of this plant be cut longitudinally one sees that it is penetrated by a canal which narrows below towards the ovary, but widens out into a funnel at the stigma, where it opens by a tri-radiate slit. The lips of this aperture bear numerous papillæ; to these the pollen-grains become attached and here commence to form their tubes. The tips of the pollen-tubes curve down into the funnel and grow along the cells which line the style-canal (fig. 313¹). Passing down this canal, which is at this time more or less mucilaginous, the pollen-tubes are led ultimately to the cavity of the ovary in which are contained the ovules.

Very different is the mode of travelling of the tubes in Grasses, of which *Avena elatior* (fig. 313²) may be taken as type. Upon the spherical ovary of this plant

two delicate feathery stigmas are inserted (*cf.* fig. 231, p. 139). The shaft of each of these stigmas consists of elongated, succulent, colourless cells, whilst the barbs of the feather are extremely delicate and filamentous in character, and have the upper extremities of the cells of which they are composed continued as little papillæ (fig. 313²). Neither in the main axis nor in the branches of the stigma are canals present. The cells fit edge to edge, and the pollen-tubes must bore a way for themselves in order to traverse the tissues in this case. The pollen-grains are attached to the

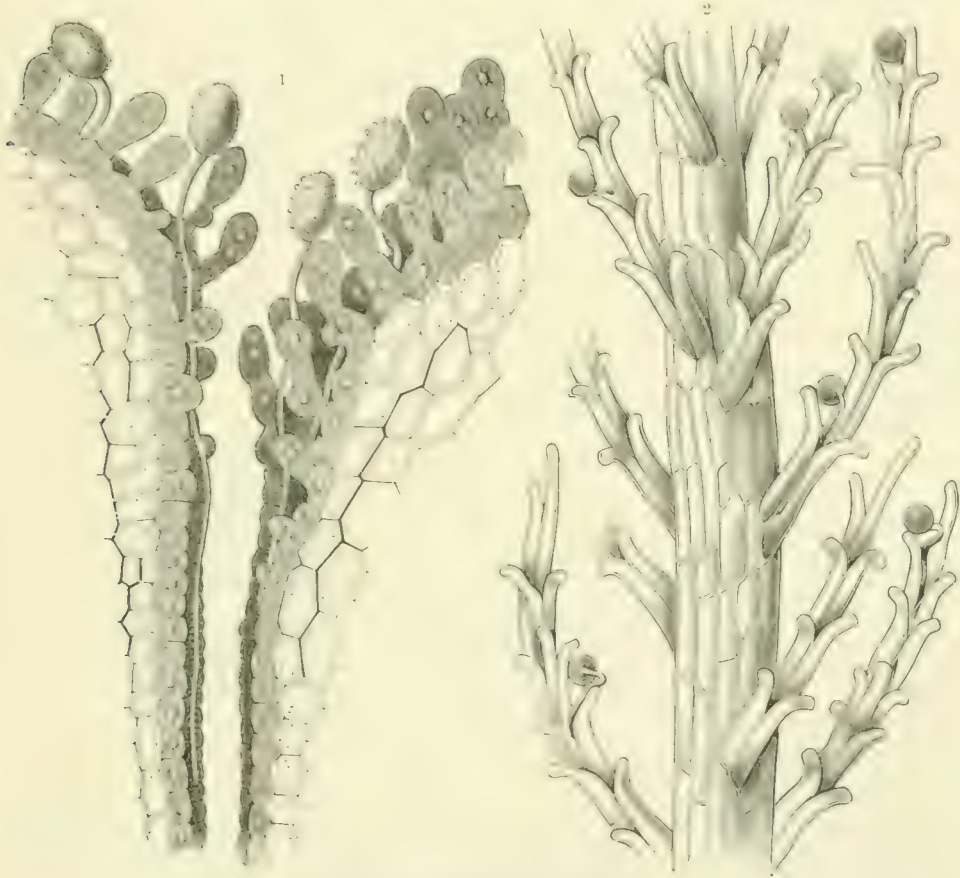


Fig. 313.—Development of Pollen-tubes.

¹ Longitudinal section of the stigma and upper portion of the style of *Lilium Martagon*. The pollen-grains present on the stigmatic papillæ are sending their tubes down the mucilaginous cells of the style-canal (after Dodel-Port); $\times 110$.

² Portion of the feathery stigma of *Arena elatior*. Pollen-grains are attached to the papillæ, and their tubes may be seen boring in between the cells of the stigmatic branches; $\times 170$.

papillæ, and as the little pollen-tubes are produced, these latter bend round so as to grow down along the inner face of the papilla. To do this they often execute very complicated curves, or they may grow spirally round the papillæ. Having reached the angle at the base of a papilla, they bore themselves a passage between the superficial cells and grow henceforward down to the ovary in an intercellular channel of their own making.

In the Grasses not only is no pre-existing canal present, but the cells between

which the pollen-tube penetrates show no demonstrable difference from their neighbours. In this respect the Grasses differ from the very large number of plants which, although they do not possess an open style-canal as in *Lilium Martagon*, have a loose axial string of mucilaginous tissue in their styles through which the pollen-tubes readily penetrate. Examples of this condition are the Solanaceæ and Scrophulariaceæ. In other cases the conducting tissue is not differentiated from its surroundings, so that the whole of the substance of the style and stigma serves for the conduction of the pollen-tubes, as in *Cistus*, *Helianthemum*, and Orchids.

A curious condition prevailing in the Cactuses has been observed in the frequently mentioned *Cereus*. Here, although a narrow style-canal is present, the pollen-tubes prefer to make their way to the ovary embedded in the tissue surrounding the canal. From this it would appear that it is of advantage for the pollen-tubes to travel thus inclosed by other tissues.

Different again is the course followed by the pollen-tubes in the Malvaceæ and in many Caryophyllaceæ. The stigmas here are in some degree like those of Grasses. As there, so here, the superficial cells are produced into long, thin-walled papillæ: to these papillæ the pollen-grains become attached by the agency of insects. The pollen-tube as it develops from the grain at once perforates the wall of a stigmatic papilla and continues its growth in the cell-cavity. The course now followed is remarkable. In the Corn Cockle (*Agrostemma Githago*) the pollen-tube often zigzags from one side of the cavity of the stigmatic papilla to the other, not infrequently taking first of all the wrong direction and bending up towards the tip of the papilla, and then bending completely round again. Having reached the base of the papilla, the tube bores through into the conducting tissue in the interior of the style, but in its further course down to the ovary grows solely between the cells, not in them. It sometimes happens that more than one tube arises from a single pollen-grain: the accessory ones, however, are for purposes of firmer attachment, and though they occasionally enter a stigmatic papilla do not continue their growth down the tissue of the style. One functional pollen-tube only is produced from each pollen-grain. In the Malvaceæ (e.g. *Malva sylvestris*) the pollen-tube entirely fills a stigmatic papilla, broadening out at the base. Ultimately the contents of the tube escape from their membrane and travel down the style in an elongated mass, destitute of wall, like the plasmodium of a Myxomycete.

Whatever be the manner of its travelling, whether with or without a wall of its own, the aim of the protoplasm of the pollen-grain is to reach one of the ovules in the ovary. Having entered the cavity of the ovary, a pollen-tube shapes a course for an ovule. The particular portion of the ovule aimed at—in the vast majority of flowering plants—is the *micropyle* (cf. vol. i. p. 644), the little receptive spot at which the coats of the ovule are discontinuous, and at which access to the embryo-sac (wherein is contained the *egg-cell*) can be gained. Only comparatively rarely is the micropyle situated immediately below the point at which the pollen-tube must enter the ovary, as represented, for instance, in fig. 208³, p. 74. Sometimes the micropyle is directed towards the side wall of

the ovary, sometimes towards the central column, as in the Star of Bethlehem (*Ornithogalum*, figs. 315^{3, 4, 5}); whilst frequently the ovule is inverted so that the micropyle faces the base of the ovary (*cf.* fig. 211⁸, p. 79). Since, in the majority of plants, several ovules are contained in a single ovary and each is fertilized by a separate pollen-tube, we find a number of tubes traversing the style, and, on their entering the cavity of the ovary, diverging to the several ovules. One would expect now to find this portion of the route to be followed by the pollen-tubes well

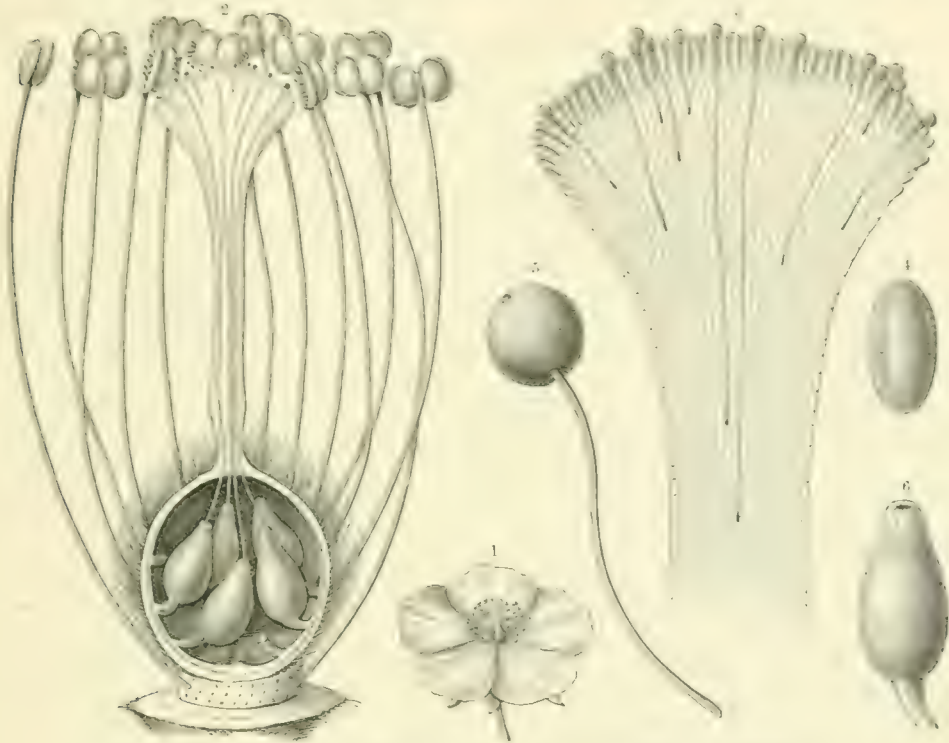


Fig. 314.—The course of the pollen-tubes in a Rock-rose (*Helianthemum marifolium*).

¹ A single flower, natural size. ² A flower, stripped of its sepals and petals, showing stigma and style and ovary in longitudinal section; the pollen-tubes are seen passing down the style to the ovary and there going one to each ovule (the tubes are indicated erroneously as going direct to the micropyles; actually they follow a more devious course, first down the inside wall of the ovary and then up to the micropyles); $\times 22$. ³ Stigma and upper portion of style in longitudinal section; shows pollen-grains attached to the stigmatic papillae and tubes penetrating the tissues; $\times 55$. ⁴ A dry pollen-grain; $\times 300$. ⁵ A moistened pollen-grain developing its tube; $\times 300$. ⁶ An ovule—which in this plant is of rather unusual form, the micropyle being at the end of the ovule distant from the point of attachment; $\times 50$.

indicated, either mechanically as by furrows and grooves, or by lines of secretory and nutrient cells leading to the micropyle. This, however, seems to be very rarely the case. As a rule such obvious guiding mechanisms are wanting. The pollen-tubes creep along the inner wall of the ovary to the places where the ovules are borne and then turn up and enter the micropyles, one pollen-tube to each ovule. The adjacent figure 314³ shows for a Rock-rose (*Helianthemum*) the whole course of the tubes from the stigma to the micropyles. As the tubes enter the cavity of the ovary they diverge and pass one to each ovule. A slight error, however, has crept into the figure in question in that the tubes are represented as passing *direct*

to the micropyles. In point of fact they follow a more roundabout course, creeping along the ovary wall, and then up the individual ovules to the micropyle.

It has been stated above that the pollen-tube enters the ovule *at the micropyle* in the vast majority of flowering plants. But this is not universally the case, as recent investigations have proved. In several of the trees belonging to the group of the Amentaceæ the pollen-tube follows an altogether different course. This



Fig. 314A.—Chalazogamic fertilization in the Hornbeam (*Carpinus Betulus*).

The drawing shows a longitudinal section of an ovule almost filling the cavity of the ovary. The micropyle (*m*) and the two integuments are shown above the apex of the nucellus (in whose cells the nuclei are indicated). Within the nucellus three embryo-sacs are represented; a pollen-tube (*p.t.*), passing down into the substance of the ovule from the placenta, follows the course of the raphe and at the base of the nucellus (chalaza) bends sharply round and enters one of the embryo-sacs; its tip penetrates to the egg-cell at the apex of the embryo-sac. Much enlarged (from a drawing by M. F. Ewart).

was first established for the case of *Casuarina*, a curious switch-plant indigenous to Australia and certain parts of Eastern Asia. A small portion of a branch of this tree is shown in fig. 69⁵ (vol. i. p. 299). *Casuarina* is wind-pollinated, the flowers being unisexual, though both male and female flowers are borne on the same individual. The pollen-grains germinate in due course on the stigma, and their tubes traverse the tissues of the style. The tubes do not, however, enter the cavity of the ovary; but continue their growth immersed in the tissues of the ovary. They thus make their way to the points of insertion of the ovules, where they enter them, and at once travel to the base or *chalaza*. From the base of the ovule the pollen-tube penetrates towards the apex of the ovule, reaching the egg-cell from below, not from above as in cases in which the pollen-tube entered the ovule by the micropyle. This type of fertilization has been termed *chalazogamic* in contradistinction to the more usual micropylar or *porogamic* method. Quite lately a renewed examination of many common trees belonging to the Amentaceous

group has shown that in several of them also fertilization is chalazogamic. This is the case in the Hazel (*Corylus*) and Hornbeam (*Carpinus*, fig. 314A), belonging to the Corylaceæ, as also in the Birch (*Betula*) and Alder (*Alnus*, fig. 314B), belonging to the Betulaceæ. In the Hazel and Hornbeam the pollen-tube, after reaching the base of the ovule, passes straight up to the egg-cell in the embryo-sac (*cf.* fig. 314A, *p.t.*) in a manner similar to *Casuarina*, but in the Birch and Alder its course is

not so direct. Here it passes by the embryo-sac on one side and then turns sharply down again, reaching the egg-cell from the same direction as it would have done had it entered by the micropyle (*cf.* fig. 314 B, *p.t.*). It is interesting to note that in many nearly allied Amentaceæ, as in the Cupuliferæ, which includes the Oak (*Quercus*), Beech (*Fagus*), and Chestnut (*Castanea*), fertilization is by the micropyle.

The following table indicates the method of fertilization as at present known in the various families comprehended in the group Amentaceæ:—

AMENTACEÆ.				Mode of fertilization.
1. Betulaceæ.				
<i>Betula</i> }	Chalazogamic. p.t.
<i>Alnus</i> }				
2. Corylaceæ.				
Hazel (<i>Corylus</i>) }	...			Chalazogamic.
Hornbeam (<i>Carpinus</i>) }				
Hop Hornbeam (<i>Ostrya</i>) }	...			Not ascertained.
3. Cupuliferæ.				
Oak (<i>Quercus</i>) }	...			Porogamic.
Beech (<i>Fagus</i>) }				
Chestnut (<i>Castanea</i>) }				
4. Juglandaceæ.				
Walnut (<i>Juglans</i>) }	...			Porogamic.
<i>Carya</i> , <i>Ptero-carya</i> , &c. }	...			Not ascertained.
5. Myricaceæ.				
Sweet Gale (<i>Myrica</i>) }	...			Porogamic.
6. Casuarinææ.				
<i>Casuarina</i>			Chalazogamic.
7. Salicinææ.				
Willow (<i>Salix</i>) }	...			Porogamic.
Poplar (<i>Populus</i>) }				



Fig. 314 B.—Chalazogamic fertilization in the Alder (*Alnus glutinosa*). Diagrammatic.

The drawing shows one half of a longitudinal section of the ovary. The wall of the ovary is thick, and has a hardened middle layer (shaded dark). At the top is the base of the style, from which the pollen-tube (*p.t.*) can be traced passing straight on through the substance of the ovary to the ovule. Entering the ovule by its point of attachment to the placenta the pollen-tube bends sharply upwards (at the chalaza) into the nucellus. It now passes by the small oval embryo-sac on the inner side, and when below the micropyle turns sharply down to the apex of the embryo-sac. The vascular supply of the ovules, which forms a column in the placenta, is shaded dark. Considerably enlarged (from a drawing by M. F. Ewart).

Many experiments have been made from time to time with a view to explaining the phenomena attendant on the wandering of the pollen-tube from the stigma to the micropyle. It has been shown that the pollen-tube is extremely sensitive to various external conditions, and that by appropriately varying these the direction followed by the tube in its growth may be controlled. Pollen-tubes are especially sensitive towards sugar-solutions, and bend out of their course towards the sugar. They also tend to grow away from the air, and show a preference for spaces saturated with aqueous vapour to such as are less humid. Of all the conditions which affect a pollen-tube, most conspicuous is the attraction which sugar exerts upon it. Various portions of the pistil exert a similar chemical stimulus on pollen-tubes, very marked being the action of the micropyle in this respect. A few of the experiments demonstrating this attractive property of stigma and ovules may be briefly described. If a fresh mature stigma be cut off and laid on a plate of gelatine, and

the gelatine in its immediate neighbourhood be dusted over with pollen-grains of the same plant, in the course of a few hours, as the pollen-tubes are developed, it will be found that they converge upon the stigma in an unmistakable manner. Pollen-tubes, even at so considerable a distance from the stigma as seventy times their own diameter, have been observed to be influenced in this way. Similar results obtain when sections of a style are employed instead of a stigma, but the attraction is not so strong. Isolated ovules laid on the gelatine exert a very marked attraction upon pollen-tubes. In one case as many as forty pollen-tubes were counted converging upon the micropyle of an ovule of *Scilla patula*. Ripe ovules ready to be fertilized exert the strongest attraction, though younger and as yet immature ovules are not without influence.

Noteworthy is the fact that an ovule is found to attract not only pollen-tubes from pollen of the same species, but of others far removed from it in point of affinity. Thus the pollen-tubes of *Scilla patula* (a Monocotyledon) were found to be attracted by the ovules of *Diervilla rosea* and *Ranunculus acer* (Dicotyledons), tubes of *Primula sinensis* by the ovules of *Antirrhinum majus* and *Digitalis grandiflora*, those of *Hesperis matronalis* by ovules of *Lonicera Periclymenum*, &c. In these experiments these strange pollen-tubes were not only attracted towards the micropyle, but actually in a few cases penetrated it. Still, no suggestion is made that anything of the nature of fertilization could be accomplished by these foreign pollen-tubes.

Nor is this attraction limited to pollen-tubes. The delicate hyphæ of several mould-fungi are similarly attracted, as also, when the surface on which the ovule rested was moistened, was that common micro-organism of decomposition, *Bacterium Termo*.

Thus it appears that substances are present in the stigma, style, and ovules, which exert a chemical attraction upon pollen-tubes, gradually leading them to the micropyle. Though it has not been possible to determine in all cases what these substances are, it is extremely probable that they are of a sugary nature. In the case of plants with chalazogamic fertilization, in which the pollen-tube, as we have seen, never enters the cavity of the ovary, it would be of interest to ascertain if the micropyle is destitute of attraction for pollen-tubes.

As stated, the attraction exerted by a given ovule or portion of a pistil is not limited to pollen-tubes of the same species, but seems common to pollen-tubes in general, and indeed to fungal hyphæ and the like. Thus it happens that instances are recorded in which fungal spores fell on the stigma, and germinating there, sent their hyphæ down the style to the ovary like pollen-tubes. And so with foreign pollen. Though it is often stated that the pollination of the stigmas of a plant A with pollen from B (a plant not allied to A) is *without result*, what is actually indicated is that no seed has been ripened by the pistil thus pollinated. Experiment has shown that, just as the pollen-tubes of one plant may be attracted towards the micropyle of an ovule of a plant of entirely different family, so pollen will germinate on the stigma of a similarly remote plant and form tubes which penetrate

considerable distances down the style, though they perish eventually. Still even should these foreign pollen-tubes actually get access to the micropyle, a fertilization of the egg-cell by the foreign spermatoplasm would be impossible, owing to the inability of the sexual protoplasm to combine outside a very narrow range of affinity. We have already seen that many plants can be fertilized either by pollen from another flower of the same species, or, wanting this, by their own pollen.

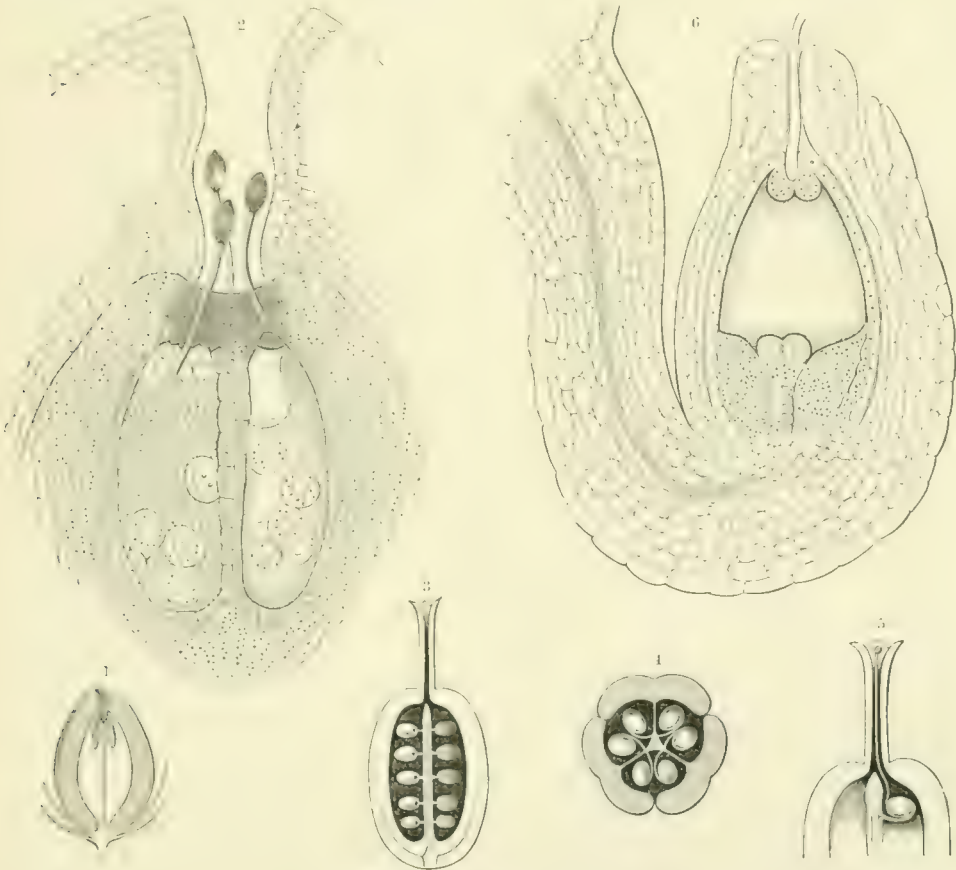


Fig. 315.—Fertilization.

¹ Longitudinal section through the ovule of *Ephedra* (a Gymnosperm); $\times 3$. ² Apical portion of a longitudinal section of the ovule of *Ephedra*, showing the pollen-grains in the micropyle producing their pollen-tubes; $\times 100$. ³ Longitudinal section through the ovary of *Ornithogalum nutans*; $\times 2$. ⁴ Transverse section of the same ovary; $\times 3$. ⁵ Longitudinal section through stigma, style, and upper portion of ovary of *Ornithogalum* showing a pollen-grain on the stigma with its pollen-tube passing down the style-canal to the micropyle of an ovule; $\times 3$. ⁶ Longitudinal section through an ovule of *Ornithogalum*. The funicle or stalk of the ovule is seen to the left, the ovule proper to the right. In the latter there is a large central space, the embryo-sac which contains certain small cells; towards the apex two together of which one is the egg-cell and the other a synergida, at the base two antipodal cells are represented. Around the embryo-sac is a layer of nucellar tissue one cell thick, whilst below, this tissue is more bulky (contents dotted). Around the nucellus are the integuments. A pollen-tube has grown down the micropyle and perforated the apex of the embryo-sac. It is represented in contact with the egg-cell and one synergida. The other synergida is not shown; $\times 100$. (Partly after Strasburger.)

Both categories of pollen-grains are competent to develop tubes and to fertilize the ovules. Under these circumstances it would be very interesting to know what exactly happens when pollen-grains of both these categories are present on one and the same stigma: whether (as is probable) both develop pollen-tubes, whether both

sets of tubes reach the ovary, or whether one set receives a check of some sort. In fact we want to know whether foreign pollen is prepotent over own pollen (where both are competent to fertilize), and if so how the prepotency is accomplished. This and a host of similar problems await solution.

Passing on now to the union of spermatoplasm and ooplasm it is first of all necessary to describe the structure of the ovule in some detail. The egg-cell which has to be fertilized forms but a small portion of the ovule. It is produced in Flowering Plants within a large cell prominently developed and termed the *Embryo-sac*. This embryo-sac is one of the cells of the central portion of the ovule known as the *Nucellus*, and this cell as the time of maturation of the ovule approaches grows much in size, in part at the expense of its neighbours. Ultimately the embryo-sac occupies a large portion of the nucellus, being still inclosed by a layer of small nucellar cells. Outside this are the integuments. They are not completely closed, but at one spot an opening (the *micropyle*) is left, the entrance by which the pollen-tube gains access to the embryo-sac. The general relations of the embryo-sac to the other portions of the ovule are shown in fig. 315^b, a longitudinal section of the ovule of *Ornithogalum*. In fig. 316 three stages of the embryo-sac of *Monotropa* are shown just at the time of fertilization. At an earlier stage the embryo-sac is a uni-nucleate cell, and before the arrival of the pollen-tube at the micropyle its contents divide up into a number of small cells, which, though devoid of cell-membranes, are readily distinguishable from one another. At the apical or micropylar end three of these cells are situated. The two uppermost, side by side, are known as the *synergidae*, whilst close below them and slightly to one side (*cf.* fig. 316) is the egg-cell, destined to be fertilized. These three cells constitute the "egg-apparatus". At the other extremity of the embryo-sac, *i.e.* at the base, three cells are present which are known as the *antipodal* cells. These, soon after their formation, develop walls around themselves and appear to play no part in subsequent phenomena. Besides these, there are two nuclei (the so-called *polar* nuclei) lying in the protoplasm of the embryo-sac, one close above the antipodals, the other just below the egg-apparatus (fig. 316¹). These two approach one another at about the moment of fertilization and fuse (figs. 316² and 316³) about midway between egg-apparatus and antipodals. They give rise ultimately to the food-material which nourishes the young fertilized egg-cell during its early stages of development.

The egg-cell and its attendant synergidæ contain each a well-marked nucleus and vacuoles. In the egg-cell the vacuole is above the nucleus (fig. 316³), in the synergidæ the vacuoles are below the nuclei (fig. 316²). The nucleus of the egg-cell is often very large. The structure and changes of cell-nuclei have already been briefly reviewed at vol. i. p. 581.

Meanwhile, in the pollen-tube changes have also taken place. Actually in the pollen-cell before the pollen-tube is produced two nuclei are present. Though both of these enter the tube one is quite sterile and soon atrophies. The other, however, surrounded by a small portion of protoplasm, but destitute of wall, constitutes the male sexual cell. It is carried, embedded in the general protoplasm of the pollen-

tube, near the tip, and so is gradually brought down to the embryo-sac. Usually this male cell divides into two, but there is no evidence to show that more than one of the daughter-cells thus produced takes an actual part in fertilization. When the tip of the pollen-tube reaches the micropyle (as in fig. 315⁶, though the contained male cells are not shown), the male sexual cells are well up to the end of the tube. The pollen-tube forces its way down the micropyle, and perforates the apex of the embryo-sac. The tip of the tube is now opened, and a male sexual cell passes out, and, traversing the synergidae, enters the egg-cell. The synergidae seem to promote this transfer of the male cell to the egg, though the precise part played by them is not fully understood. With the passage of the male cell the synergidae collapse and shrivel; their part is played. The anterior of the two male cells of the pollen-tube enters the egg-cell, the other one being possibly of the nature of a reserve in case of accident. Occasionally, it also enters, and has been observed in the egg, though probably this is an accidental circumstance. After the entrance of the male cell its nucleus approaches the female (egg-) nucleus and fuses with it. This fusion constitutes the act of fertilization. Though this nuclear fusion is the most characteristic feature of fertilization it may well be that the other elements which enter the egg-cell with the male nucleus likewise fuse with the protoplasm of the egg. So far, observations have not absolutely determined the fate of these less conspicuous elements. On the other hand, it is possible that these subordinate elements serve in large part merely as food-material for the egg. As yet the time has not arrived to speak decisively on these points.

The fertilized egg-cell, which we may now term the *embryonic cell*, soon gives indication of the change which it has undergone. It secretes a cell-wall around itself. Had it not been fertilized the egg-cell would have remained naked and inactive, and ultimately would have perished.

In the account of fertilization of the Angiosperm just given, the main facts have been related; and although from time to time fresh observations come to light, it is hardly probable that the main outlines as given above will be overthrown. That a



Fig. 316.—Embryo-sac of *Monotropa*.

Three stages are shown just preceding fertilization, in the order 1, 2, 3. In each of them we see the group of antipodal cells at the base, and the egg-apparatus at the apex. 1 and 2 show the two synergidae side by side and the egg-cell adjacent to them. In 3 the synergidae are on the left, seen through one another, both their nuclei showing; the egg-cell on the right. The process of fusion of the so-called polar nuclei is shown in the figs.; in 1 they are not yet detached from their respective groups, in 2 they have approached one another, in 3 they are in process of fusion.

fuller knowledge of the details will be obtained is exceedingly probable, in view of the active state of research into these processes.

In the *Gymnosperms*, the group of Flowering Plants with exposed ovules, though the essential facts of fertilization—the fusion of the male sexual cell with the female sexual cell (egg)—are the same as in the *Angiosperms*, just described, in many subordinate points they exhibit marked differences. The male flowers of *Gymnosperms* produce stamens with anthers in which pollen-grains are developed much as in *Angiosperms*. The arrangements, however, associated with the production of ovules are simpler than in the *Angiosperms*, and recall to some extent the characters presented by certain Ferns. In the Ferns and other *Cryptogams* it will be remembered that fertilization is under water, whilst in *Phanerogams* this is accomplished through the medium of the air (*cf.* p. 71). The spermatozoids of the *Cryptogams* reach the egg-cell in the oogonium or archegonium by swimming; they are naked protoplasmic masses, and need no enveloping and protective cell-wall. It is otherwise in the *Phanerogams*, where aerial fertilization obtains. Here a membrane around the spermatoplasm is of great value; it serves to protect the contents of the pollen-grain during its journey through the air, and afterwards, in connection with the pollen-tube, is of the utmost value in conveying the male sexual cell to the egg. Notwithstanding the resemblance presented by the female flowers of many *Gymnosperms* to certain *Cryptogams*, they agree with the *Angiosperms* in the fact that the male cell is brought to the egg-cell by means of a pollen-tube. In this point all *Gymnosperms* agree, *i.e.* the *Cycads*, *Conifers*, and *Gnetaceæ*.

The ovules of *Gymnosperms* show the grosser characters of those of *Angiosperms*. In fig. 335⁷ is shown a scale from a female flower (cone) of the Scotch Pine (*Pinus sylvestris*). Right and left at its base are the ovules, two in number. Each ovule exhibits a central nucellus and a conspicuous integument surrounding it, leaving a wide, funnel-shaped micropyle giving access to the tip of the nucellus (*cf.* also fig. 208⁸, p. 74, representing an ovule of *Cycas*). Within the nucellus a large cell becomes marked out, as in *Angiosperms*; this is the embryo-sac. The embryo-sac becomes filled with an extensive tissue, the endosperm, and produces at its apical end (towards the micropyle) a number of egg-cells. These vary in number from 2–15 in various *Gymnosperms*, but in any case they are all assembled together beneath the micropyle. Associated with each egg-cell is a neck, recalling that structure in the archegonium (or amphigonium) of Ferns (*cf.* p. 67). Fig. 315² shows the tip of a gymnospermic ovule in section, considerably enlarged. Note the funnel-shaped micropyle (with germinating pollen-grains in it) and two large, oval egg-cells in the endosperm below. The slight shading above the tips of the two egg-cells indicates the necks. The contents of the egg-cells in this figure have already given rise to several cells, as in the stage represented fertilization has just occurred. The cells here shown in *Ephedra* (fig. 315²), or in most other *Gymnosperms* a limited number of cells (often four) cut off at the base of each egg-cell, develop into little embryos, of which, however, ultimately one only survives for each

seed. A characteristic feature, occurring shortly before fertilization, is the cutting-off of a small cell from the summit of the egg-cell. This little bi-convex cell (shown at the tip of the right-hand egg in fig. 315²) is known as the "ventral canal-cell". A similar cell is cut off in the Ferns, &c., and lies at the base of the neck of the archegonium just above the egg-cell. It is afterwards absorbed.

From a comparison of the structures in the ovule of a Gymnosperm with those arising on the Fern-prothallium, or Moss-plant, it seems probable that the egg-cell, with its neck in the former, corresponds to the archegonium of the latter, though the archegonium in the Gymnosperm is somewhat reduced when compared with the exposed archegonium of Ferns and Mosses.

The number of egg-cells (=archegonia) produced in the ovule of a Gymnosperm is various. In the Spruce Fir and Pine there are from 3 to 5, in the Cypress and Juniper 5 to 15. In the Firs and Pines the egg-cells are well isolated from one another by layers of endosperm, in which they are embedded; in Cypresses and Junipers the egg-cells are all in immediate contact, forming a rosette-like cluster at the top of the endosperm under the micropyle. The tissue in which they lie embedded, the endosperm, is in Gymnosperms pretty extensive, and being well-stocked with food-materials, forms, after fertilization, a nutritive bed for the young developing embryos, and is ultimately absorbed by them.

In the Angiosperms, on the other hand, the ovules are not exposed on open scales, as in Gymnosperms, but inclosed in definite chambers, the ovaries. Pollen is brought to the stigma (not to the micropyle, as in Gymnosperms), and fertilization is accomplished by the development of pollen-tubes, which penetrate the tissues of the style to the ovules. In Gymnosperms there are no ovaries or styles or stigmas. Pollen is brought by the wind direct to the micropyle of the ovules. Various arrangements exist for bringing the pollen-grains into the micropyle and for holding them there. Just at the time when pollen is liberated from the male flowers the micropyle is opened wide, and its lining cells are rendered sticky by a mucilaginous secretion, so that the pollen brought by the wind sticks to it. This mucilage often projects as a little droplet from the micropyle, and in it the pollen-grains are caught; as this drop gradually dries up and contracts the pollen-grains are sucked into the micropyle, so that the grains come to lie right on the tip of the nucellus of the ovule, from which point they germinate, putting out their tubes (*cf.* fig. 315²). These drops of mucilage can be well seen in early spring on the exposed ovules of the Yew-tree (*Taxus baccata*). This plant is dioecious, and on the female plants the tips of the ovules project from a few scale-like wrappings, which envelop the base of each ovule (*cf.* figs. 336² and 336³). At the time when the male flowers are intrusting their pollen-grains to the wind (usually in March) one may see the female plants, on a sunny morning sparkling in the sunshine as it were with dew-drops. These "dew-drops" are in reality droplets of mucilage, excreted from the micropyles of the ovules, awaiting the chance deposition by the wind of pollen-grains. By and by they dry up and the entangled grains are sucked into the micropyle. In Gymnosperms it is the micropyle, not the stigma, which is pollinated.

After the entrance of the pollen-grains into its mouth the micropyle contracts somewhat, so that the pollen is, so to speak, imprisoned. In Gymnosperms the active development of pollen-tubes only occurs some considerable time after pollination. In the Pine the pollen-grains put out short tubes soon after pollination, but these tubes remain dormant from the spring in which pollination takes place through the summer, autumn, and winter, and only continue their growth after the lapse of about a year. Meanwhile changes take place within the ovule leading to the production of the archegonia with mature egg-cells. Actual fertilization occurs about thirteen months after pollination.

The contents of the pollen-cell, before it leaves the anther (Pines and Firs), or shortly after its reception in the micropyle (*Taxus* and *Cupressus*), divides several times, a number of small cells being cut off at one side of the grain and their substance being separated from the rest of the contents of the grain by cell-membranes. Of these small cells one is the male sexual cell, and ultimately effects fertilization. The big cell (known as the "vegetative cell") produces the pollen-tube. The male sexual cell ("generative cell"), becoming free from its attachments (membranes), passes into the pollen-tube, where it divides into two cells. Ultimately one of these cells fertilizes an egg-cell (the other not being required). In the Juniper, where one pollen-tube fertilizes more than one archegonium, both these generative cells—and possibly others, the result of their further division—would appear to be utilized. The generative cells are carried along with the tube near its growing tip—much as in Angiosperms. Bit by bit the pollen-tube penetrates deeper into the substance of the ovule which forms the floor of the micropyle. Ultimately the tube reaches the neck of an archegonium, and pushes in between the neck-cells, carrying the male cells to the mature egg-cell. In the Cypress and Juniper, where several egg-cells are clustered close together, the tip of the tube widens out, sending a little branch to each of the egg-cells (archegonia), every one of which it is competent to fertilize. In the Pine, Firs, and other Gymnosperms, distinct tubes from separate pollen-grains penetrate to the several archegonia.

Fertilization happens much as in Angiosperms (described on p. 417): the male cell enters the egg-cell, and the male nucleus fuses with the female nucleus. Probably the other elements of the male cell are also taken up by the egg-cell. Indeed, the whole process of pollen-tube development and fertilization is exceedingly similar to these events as described in the Angiosperms. A chief point of difference consists in the absence of distinct cell-walls between the cells which arise in the pollen-grain of the last-named group.

The *development of the embryo from the fertilized egg-cell* is different in Angiosperms and Gymnosperms. In *Angiosperms* the egg-cell, after surrounding itself with a cell-wall, becomes partly attached to the apex of the embryo-sac. It divides by a transverse wall into two cells, one directed towards the micropyle, the other towards the base (chalazal end) of the embryo-sac. The upper (*i.e.* micropylar) of

these two cells stretches, and is repeatedly segmented; thus a string of cells is formed, known as the *suspensor*, bearing at its lower extremity the *embryo-cell*, which gives rise to the greater portion of the young plant. The suspensor, by its elongation, brings the embryo-cell well down into the cavity of the embryo-sac, where it is embedded in the substance of the endosperm which has meanwhile developed. The nutrition of the young plant is thus assured during its early stages. In many Parasites and in Orchids the full-grown embryo shows but little differentiation, and is little more than a mass of cells exhibiting no distinction of stem and leaf-structures; but in the great majority of Angiosperms it soon shows a differentiation into parts—into a little root at one end and a stem at the other, with the rudiments of leaves (*cf.* vol. i. p. 599, figs. 141¹ and 141²). These leaves, the *cotyledons*, are a conspicuous feature of the embryo, and in several plants they are coloured green by a precocious development of chlorophyll in their tissues (e.g. *Styphnolobium japonicum*). In a large number of plants, as, for instance, the Apple and Oak, Bean and Pea, garden Nasturtium (*Tropæolum*) and Water Chestnut (*Trapa*, *cf.* vol. i. p. 607, figs. 144^{1, 2, 3, 4, 5, 6}), the cotyledons become much enlarged and succulent, and take up large quantities of food-material, which remains stored up in them as reserve-material for the further development of the young plant at germination. When this happens the cotyledons usually come to fill the whole cavity of the seed right up to the integument (*testa*). In the majority of plants, however, the cotyledons remain small and thin, and do not take up the whole reserve of food-material which envelops the embryo. Under these circumstances the embryo is provided with a special reserve-tissue, destined for its consumption when it is separated from the mother-plant. This tissue is analogous to the yolk of a bird's egg, and consists of a tissue of cells filled with fat, starch- and proteid-granules. This food-tissue is variously known as *endosperm*, *albumen*, &c., but the terminology associated with it does not reflect great credit upon the Botanists who are responsible for the introduction of the various terms.

The starting-point for this *reserve-tissue* consists of the nucleus which arises in the embryo-sac from the fusion of the so-called *polar nuclei* (represented in figs. 316^{1, 2, 3}, and described on p. 416). Around these nuclei a certain amount of protoplasm collects, and after their fusion into the so-called *definitive nucleus* (fig. 316³), a very active cell-division sets in, which results in the formation of a parenchymatous tissue which occupies the embryo-sac and becomes filled with food-materials (fat, starch, and proteids). This tissue is the already-mentioned *reserve-tissue* of the seed or *endosperm*. Most frequently, as we have stated, the embryo enters on a resting period embedded in or adjacent to this reserve, and absorbs it at germination. In other cases, as in the Bean, Oak, &c., as mentioned, the cotyledons of the embryo forthwith take up all this food, so that when the resting-stage comes on, the greatly swollen embryo fills the whole cavity of the seed. This former class of seed is spoken of as *albuminous*, the latter as *ex-albuminous*. There is just this difference between albuminous and ex-albuminous seeds: in the former the embryo only takes up the food-material at germination, in the latter, relatively

early, before the seed enters on its resting-stage. The ultimate fate of the food-material is the same in both cases, *i.e.* to nourish the young plant.

The relations of the *embryo* to its *reserve-tissue* are very various. In many plants, *e.g.* Pimpernel, Wood Sorrel, Snapdragon, and Strawberry-tree (*Anagallis*, *Oxalis Acetosella*, *Antirrhinum majus*, *Arbutus Unedo*, *cf.* figs. 317^{3, 4, 5, 6, 7, 8, 9, 10}), the straight embryo lies embedded in its reserve-tissue. The same relations obtain in the Rue (*Ruta graveolens*, *cf.* figs. 317¹ and 317²), the embryo here being slightly bent; whilst in *Phytolacca decandra* (fig. 317¹¹), on the other hand, the embryo is outside its reserve-tissue, and curved around it like a horse-shoe. In Sapindaceæ and Chenopodiaceæ the embryo is spirally twisted. In the Grasses it is laterally placed to its reserve-tissue (*cf.* vol. i. p. 599, figs. 141³ and 141⁴), and the manner in which it utilizes its reserve has been already fully described in vol. i. p. 604.

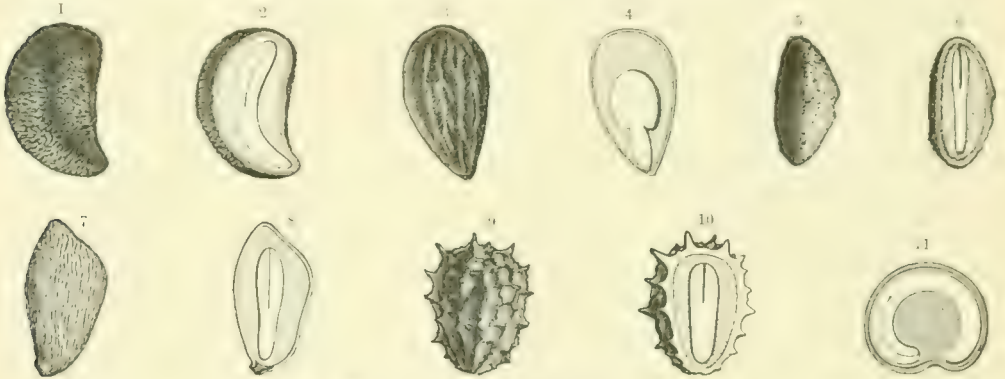


Fig. 317.—Seeds with a Reserve-tissue.

¹ *Ruta graveolens*, the intact seed. ² Longitudinal section of the same. ³ *Oxalis Acetosella*, intact seed. ⁴ Longitudinal section of the same. ⁵ *Anagallis phœnicea*, intact seed. ⁶ Longitudinal section of the same. ⁷ *Arbutus Unedo*, intact seed. ⁸ Longitudinal section of the same. ⁹ *Antirrhinum majus*, intact seed. ¹⁰ Longitudinal section of the same. ¹¹ Longitudinal section of seed of *Phytolacca decandra*. (After Baillon.)

Both the embryo and its reserve-tissue increase at the expense of the tissue immediately external to the embryo-sac: and in the ripe seed very slight traces of this tissue are to be found. Only in relatively few seeds is food stored in this peripheral tissue (*i.e.* in the tissue of the nucellus between the integument and embryo-sac). Under these circumstances this nucellar tissue assumes very much the character of the more usual reserve-tissue (endosperm) which is formed *within* the embryo-sac. Its cells become filled with fat, starch, and proteids, which serve later on as food-material for the young plant. Reserve-tissue when stored *within* the embryo-sac is termed *endosperm*; this, which arises external to the embryo-sac is, in contradistinction, termed *perisperm*.

It is worthy of note that a formation of reserve-tissue does not take place in ovules which are not fertilized. The act of fertilization obviously exerts an influence not limited to the embryo. One may compare this influence to the impulse generated when a stone is thrown into still water. Just as waves travel in ever-widening circles from the centre of disturbance, so it is with the changes in the ovule: first, changes are noticeable in the egg-cell, then successively in the embryo-sac,

integuments, in the carpels, and, finally, in the flowering axis which bears the whole of the structures concerned. These changes, which become manifest in the form of growth, are executed on a definite plan in every plant, and depend on the peculiar constitution of the protoplasm. The aim of these growth-changes is not difficult to determine. The new organism which has arisen from fertilization must be adequately provided for the future; it is detached sooner or later from its parent-

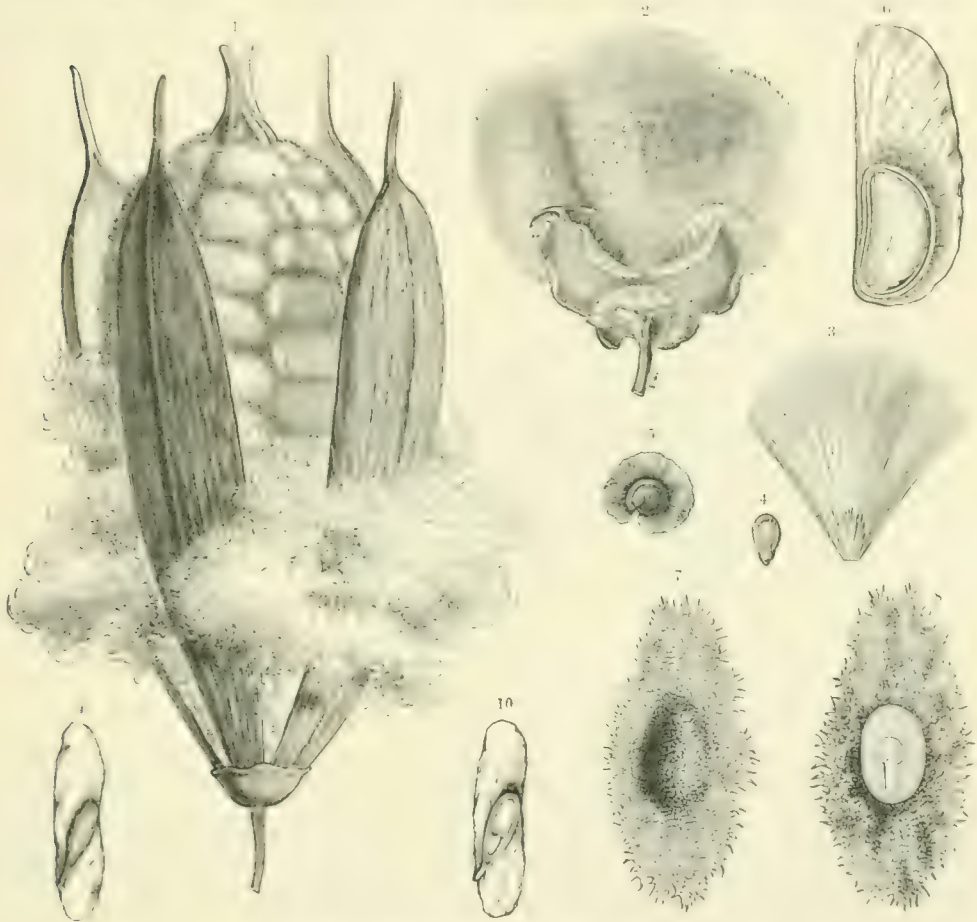


Fig. 318.—Seeds with winged and hairy appendages.

- ¹ Dehiscent fruit of *Eriodendron*; the seeds embedded in a hairy investment are visible between the valves. ² Dehiscent fruit of *Gossypium herbaceum*; the mass of seeds is contained in a hairy investment protruding from the valves. ³ Seed of Aspen (*Populus tremula*) with silky appendage. ⁴ The same seed stripped of its silk. ⁵ Winged seed of *Lepigonum marginatum*. ⁶ Longitudinal section of the winged seed of *Vochysia*. ⁷ Winged seed of *Cinchona*. ⁸ Longitudinal section of this seed. ⁹ Winged seed of *Cedrela Toona*. ¹⁰ Longitudinal section of same. ⁴⁻⁸ magnified. (Partly after Baillon.)

plant, and has to establish itself in a new place. The embryo requires special equipment for its journey and for its start in life; it requires a means of dispersal and protection against attacks from animals so long as it remains attached to the parent-plant, it requires also protection against unfavourable climatic conditions. These various equipments are provided by peculiar changes in the integument, carpels, and receptacle, changes which are initiated at fertilization.

The integuments of the ovule are altered into the *seed-coat*, which often exhibits a differentiation into two layers. The inner layer takes the form of a delicate, colourless membrane which is rarely hardened, or of a mucilaginous, readily-swelling layer. The outer seed-coat or *testa* shows, however, a great variety of form. It usually consists of several layers of cells, the successive layers of which are frequently very differently fashioned. Sometimes they are soft and membranous, sometimes rigid and parchment-like, woody or horny, whilst in other cases they may be succulent and fleshy, or converted into a mucilaginous, sticky envelope. The outmost layer of the testa is usually brown, gray, and black, more rarely yellow, white, or red in colour. The significance of the various slimy layers, which on moistening become sticky, of the little pits and furrows, warts, spines, and the like in promoting the firm anchoring of the seed on its germinating bed has already been fully pointed



Fig. 319.—*Salix polaris* with opened fruits showing masses of hairy seeds escaping.

out (cf. vol. i. pp. 614-620). Many seeds, in order that they may be distributed by the wind, develop from the outmost layer of the testa wing-like appendages, as, for instance, in the seeds of the Caryophyllaceous *Lepigonum marginatum* (see fig. 318⁵), in those of the Cinchona-tree (*Cinchona*, figs. 318⁷ and 318⁸), in the tropical *Vochysia* (fig. 318⁶) and *Cedrela* (figs. 318⁹ and 318¹⁰), and many others. This just-mentioned *Vochysia*-seed is also characterized by the curious wrapping of the cotyledons upon one another (fig. 318⁶). Often, again, for the same purpose, the superficial cells of the testa grow out, forming a plume or plexus of silky or cottony hairs, as in the Indian species of Cotton-plant (*Gossypium herbaceum*, fig. 318²), and in the cotton-producing *Eriodendron* (fig. 318¹). In the seeds of the Oleander (*Nerium Oleander*) the hairs at the apex are longer than those at the base, whilst in the Willow-herb (*Epilobium*) a delicate tuft of long silky hairs is developed at the apex only.

In a considerable number of plants there is developed from the base of the seed, or from its funicle, a curious and special structure, which by the time the seed is ripe envelops the seed like a mantle. This structure is known as the *Aril*. These arils

show very various characters, just as the testa itself may do. In the Willow (*Salix*, fig. 319) and Poplar (*Populus*, figs. 318² and 318⁴) it consists of long, delicate silky hairs: in many Passifloraceæ, Sapindaceæ, and Celastrineæ—amongst others, in the well-known Spindle-tree (*Euonymus*), it forms a fleshy, succulent investment, often coloured bright red or orange, whilst in the Myristicaceæ it forms a curious, lacinated sheath. In the Nutmeg (*Myristica moschata*) the seed proper constitutes the nutmeg of commerce, whilst the mace is the aril which grows around this seed. When these accessory structures of the seed are only developed locally as little ridges or bumps at the base of the seed, or on the funicle, they are known as *caruncles*. A well-marked, fleshy cock's-comb-like caruncle is formed on the seeds of the Celandine (*Chelidonium majus*). When the swelling is limited to the point of attachment of the seed to its funicle, one speaks of a *hilar caruncle*, as is seen in the Pansy (cf. figs. 320¹ and 320²). The spot where the seed is attached to its stalk is known as the *hilum*, and is readily seen, even when distinguished by no special swelling or caruncle, on a detached seed. It is usually a well-defined area, coloured differently from the rest of the testa, sometimes projecting, sometimes slightly excavated, and not infrequently having the form of a well-marked groove (see fig. 320⁵). At the place where separation has occurred there is a kind of scar, the *hilar scar* (sometimes called the *omphalodivium*). The spot occupied by the micropyle is often recognizable on the ripe seed, and may be termed the *micropylar scar*. It usually appears as a little hole or pin-point depression bordered by peculiar tissue. In curved (campylotropous) seeds, the micropylar and hilar scars are seen near together, but not so close as to be inseparable (figs. 320⁶ and 320⁷; in 320⁶ the point indicates the position of the micropylar, the excavation that of the hilar scar). In the Castor-oil plant (*Ricinus communis*, figs. 320³ and 320⁴), the lips of the micropyle undergo considerable growth, forming a little cushion or micropylar caruncle, very conspicuous at the top of the seed.

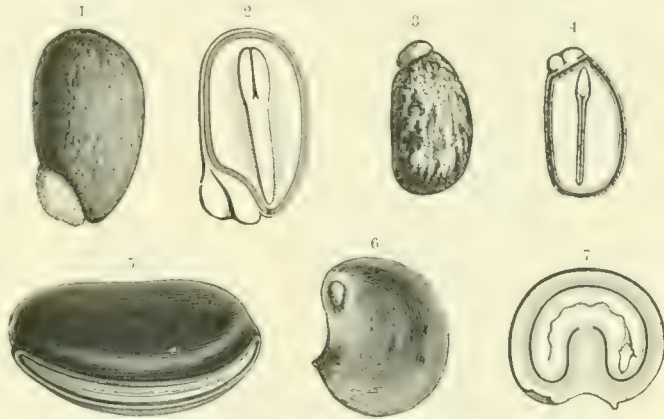


Fig. 320.—Seeds with caruncles and hilar scars.

¹ Seed of *Viola tricolor*. ² The same in longitudinal section. ³ Seed of *Ricinus communis*. ⁴ The same in longitudinal section. ⁵ Seed of *Physostigma venenosum*. ⁶ Seed of *Anamirta Cocculus*. ⁷ The same in longitudinal section. (After Baillon.)

Corresponding to the externally visible hilar and micropylar scars is a curious internal structure of this portion of the seed-coat. This will be more intelligible when it is explained that in many cases the water needed by the resting embryo for its further development can only be absorbed at these spots. The tissue here,

indeed, serves as a mechanism for supplying the embryo with moisture from the germinating bed. For its successful operation it is necessary that the seed should be favourably situated upon the soil, in other words, that these portions of tissue which conduct water to the embryo should be in contact with the damp earth. Such a position is promoted by the fact that in cases of the kind under discussion the seed is so formed and its centre of gravity so adjusted that in falling the hilar scar generally comes to lie underneath. The tissue here is more or less porous and provided with lacunæ, so that water can be taken up and transmitted to the

embryo. Not infrequently it consists of loose stellate cells, and water is absorbed from the environment as by a sponge and placed at the service of the deeper-lying regions of the seed, especially the embryo.

In those seeds, on the other hand, in which water is not absorbed at definite spots but over the whole surface, there exist scattered over the surface between the thickened impervious cells, which form the greater portion of the investment, special strings of cells or minute canals which at the proper time are permeable and serve for the taking up of water. Thus, for instance, in the hard, round, black seeds of the Indian Shot (*Canna*), the testa, consisting as it does



Fig. 321.—1 Branch of Mezereon (*Daphne Mezereum*) with berries. 2 Fruiting branch of the Lime (*Tilia*) with downy hairs investing the nut-like fruits.
 2 Longitudinal section through a fruit of the Lime. 1 and 2 natural size.
 2 magnified.

of an outer layer of thick-walled palisade-cells with several layers of transversely-stretched stony cells beneath, constitutes an exceedingly strong protection for the embryo. But over the whole surface of the seed are distributed tiny depressions, at the base of each of which a stomate opens. Each of these stomates leads into a canal of minute proportions traversing the layers of the testa and adequate for taking up water at germination.

Intimately connected with the developing seeds is the structure in which they are contained, and in which they were originally fertilized. This is known at the time of fertilization as the *pistil* or *ovary*, and later, when the seeds are ripe, as the

pericarp, seed-capsule, or case. As a rule this structure is known to Botanists as the *fruit*, though this designation is open to criticism. In the broad sense the fruit in Phanerogams should include everything which undergoes alteration after fertilization either in the flower or flowering axis. All these changes take place in the parts in question for the purpose of promoting the interests of the embryo, and properly equipping it when the time comes for its severance from the parent plant, consequently the whole of the structures which participate in this object should be regarded as the fruit. From this point of view the seed-case or pericarp (derived from the pistil) constitutes only a portion of the fruit. Since, however, the seed-

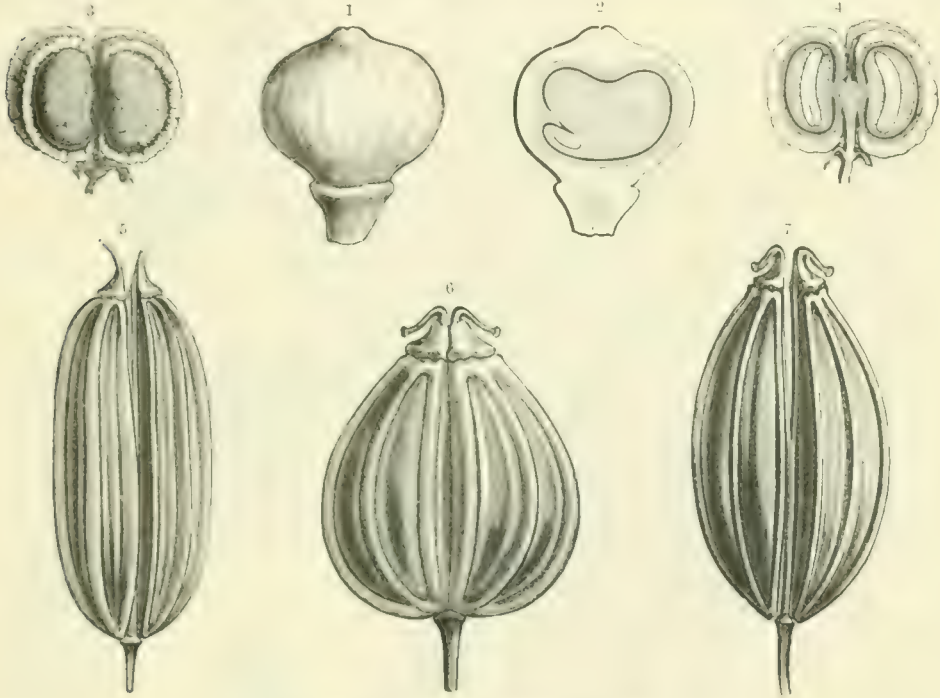


Fig. 322.—Indehiscent fruits and schizocarps.

¹ Drupaceous Nut of *Fumaria*. ² The same in longitudinal section. ³ Indehiscent fruit of *Callitriche*. ⁴ The same in longitudinal section. ⁵ Schizocarp of *Foeniculum aromaticum*. ⁶ Schizocarp of *Petroselinum sativum*. ⁷ Schizocarp of *Carum carvi*. All the figs. enlarged. (After Baillon.)

case in a very large number of cases approximates to and essentially constitutes the whole fruit, we will not press our quarrel with the descriptive botanists to the point of pedantry, but having made our protest fall into line with the usual terminology.

Types of Fruit.—When the seed-case derived from the pistil becomes altogether fleshy and succulent, the fruit is termed a *Berry*. From inferior pistils arise inferior berries. From superior pistils superior berries. The berries of the Bitter-sweet (*Solanum Dulcamara*), of the Deadly Nightshade (*Atropa Belladonna*), of the Barberry (*Berberis vulgaris*), and of the Vine (*Vitis vinifera*) are superior: those of the Mistletoe (*Viscum album*), and of the Gooseberry (*Ribes Grossularia*) are inferior. The berry of the Mezereon (*Daphne Mezereum*) is also superior, but is

peculiar in that the flesh is contributed not only by the pericarp proper (fruit-wall), but also by the outmost layer of the seed-coat. It is the inner layer of the seed-coat which here gives rise to the stone.

When the outer part of the pericarp is fleshy, and the inner part which immediately invests the seeds stony, the fruit is called a *Drupe* or stone-fruit. The

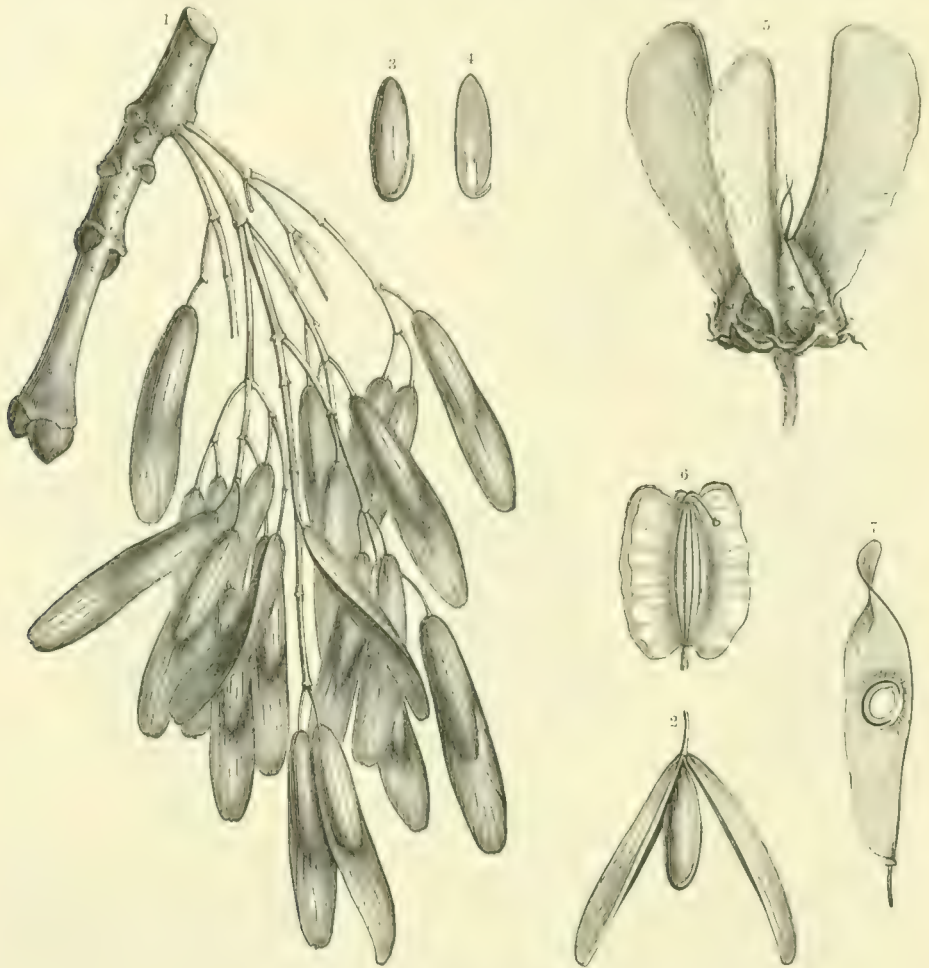


Fig. 323.—Winged Fruits.

¹ Cluster of fruits of the Ash (*Fraxinus excelsior*). ² A single fruit artificially opened. ³ Seed of *Fraxinus excelsior*. ⁴ The same seed in longitudinal section. ⁵ Fruit of *Banisteria*. ⁶ Fruit of *Angelica sylvestris*. ⁷ Fruit of *Ailanthus glandulosa*, the central, seed-containing portion seen in section. (Partly after Baillon.)

majority of drupes, e.g. the Sloe (*Prunus spinosa*), and Cherry (*Prunus avium*), contain only a single stone and seed. That of the Buckthorn (*Rhamnus*) contains two stones, each of which contains a seed, whilst that of the Elder (*Sambucus nigra*), usually described as a berry, is in reality a drupe containing from 2–4 stones each with one seed.

In a very large number of fruits the pericarp is entirely dry. These *dry* fruits

may be distinguished into *Indehiscent fruits*, *Schizocarps*, and dry *Dehiscent fruits*. The indehiscent fruit never opens spontaneously. When ripe it comes away with the inclosed seed and is concerned in the dispersal and establishment of this seed. The indehiscent fruit is termed a *Nut* when it arises from a pistil constituted of more than one carpel, as in the Lime (*Tilia*, figs. 321² and 321³), an *Achene* when produced from a monocarpellary pistil. When the contained seed is entirely fused with the lining of the fruit-wall, as in Grasses (*cf.* vol. i. p. 599, fig. 141³), the fruit



Fig. 324.—Flowering branch of *Banksia serrata* with thick-walled dehiscent capsules. (After Baillon.)

is termed a *Caryopsis*. Sometimes the wall of the nut consists of an outer more fleshy layer, and an inner harder layer after the manner of a drupe. Such a fruit, as in the Fumitory (*Fumaria*, figs. 322¹ and 322²), is known as a drupaceous nut. As a rule the nut is uni-loculate and contains but a single seed; and this notwithstanding the terms of our definition, according to which a nut is the product of a multi-carpellary ovary. Actually in development all the chambers but one (which contains the ripe seed) atrophy. Only rarely are nuts multilocular, as in the Water-star (*Callitriche*, figs. 322³ and 322⁴) which has a 4-chambered nut and forms a transition to the schizocarp.

The *Schizocarp* may be regarded as consisting of a number of Achenes united together. Two or more carpels, each containing a seed, remain joined together during

ripening, and only later, when the seed is ripe, do they separate from one another, as though the original fruit had been cut into its component parts by a sharp knife. Each of these components (known as *Mericarps*) remains indehiscent like an achene, and is distributed with its contained seed. As a type of these schizocarps the Mallow (*Malva*) may be taken. In the Umbelliferae the two mericarps into which the schizocarp splits remain for a long time suspended from the tips of a forked prolongation of the axis, as in the fruits of the Caraway (*Carum carvi*, fig. 322⁷), Parsley (*Petroselinum*, fig. 322⁶), and Fennel (*Foeniculum*, fig. 322⁵).

As already mentioned, the pericarp of many indehiscent fruits assists in the dispersal and establishment of the inclosed seeds. This may happen in two ways. The surface of the fruit may bear hairs, curved bristles, or hooked spines which become attached to the coats of animals; or wings, plumes, &c. may be produced, allowing the fruit to be readily borne away even by the gentlest of breezes. Such winged fruits are termed *Samaras*, and many forms of them are distinguished by the descriptive botanist. To these remarkable fruits, however, we shall return in detail later on when dealing with the dispersal of plants; it will suffice here to indicate briefly a few forms. The fruits of the Ash (*Fraxinus excelsior*) are shown in figs. 323^{1, 2, 3, 4}. The pericarp of each consists actually of two carpels joined together; it is continued into a well-marked membranous wing. Fig. 323⁷ represents the samara of the Tree of Heaven (*Ailanthus glandulosa*) which is continued below and above the seed-containing portion into a thin, spirally-twisted wing. In the fruit of the Umbelliferous *Angelica sylvestris* (fig. 323⁶) each half (mericarp) shows a sinuous wing-like fringe on either side, whilst in *Banisteria* (fig. 323⁵) there projects from the back of each component a membranous continuation resembling a butterfly's wing.

Dry dehiscent fruits are also known as *Capsules*. When ripe their pericarp, which is quite dry, opens and liberates the seeds in a variety of ways. The empty capsule remains, as a rule, on the parent plant, or comes away in pieces (*valves*) at the time of dehiscence. In neither case, however, has the pericarp any further concern with the seeds after these are once liberated. These capsules are the commonest class of fruit, and as their structure is characteristic of many genera, their various modifications have received distinctive names. When the pericarp arises from a single carpel, and at ripening opens along one side, along the so-called *ventral suture*, whilst the opposite side (the *dorsal suture*) is unsplit, or but partially, one speaks of the fruit as a *Follicle*. As a rule several follicles are collected together in a cluster at the end of the flower-stalk, as, for instance, in Monkshood (*Aconitum*) and in the Star Anise (*Illicium anisatum*, cf. fig. 325¹); more rarely are they solitary, as in certain species of Larkspur (*Delphinium*). In the Proteaceae, also, a single follicle arises from each flower, and in the Australian "Wooden Pear" (*Xylomelum pyriforme*, fig. 325²), belonging to this order, the huge and extraordinarily thickened follicle splits completely down the ventral and halfway down the dorsal suture. In *Banksia*, also, of which a head with fruits is shown in fig. 324, the follicles are very hard and woody.

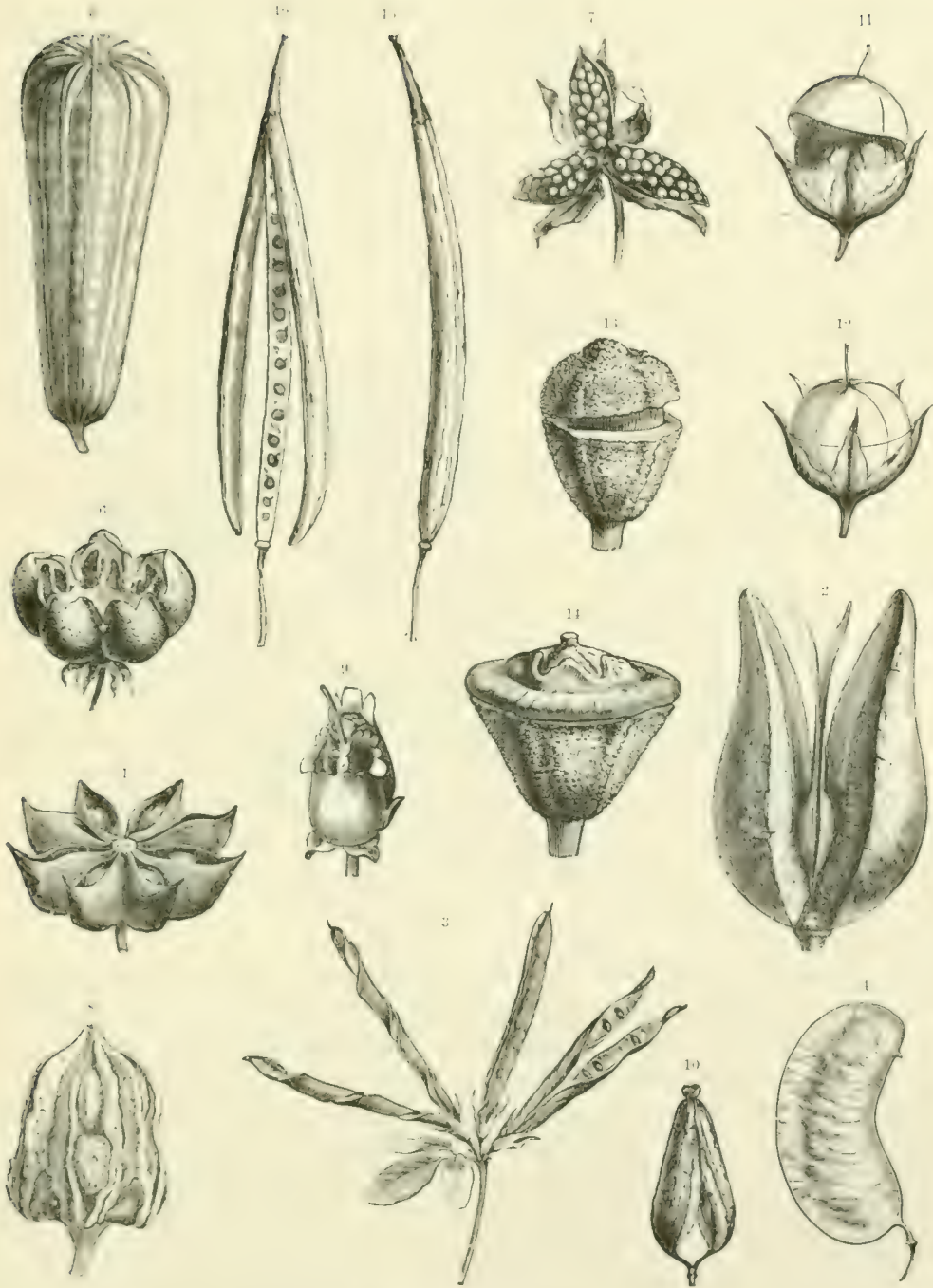


Fig. 325.—Various Capsular Fruits.

1 Follicles of *Illicium anisatum*. 2 Follicle of *Xylometum pyriforme*. 3 Pods of *Lotus corniculatus*. 4 Pod of *Cassia angustifolia*. 5 Capsule of *Aristolochia*. 6 Capsule of *Ruta*. 7 Capsule of *Viola*. 8 Capsule of *Oxalis*. 9 Capsule of *Antirrhinum*. 10 Capsule of *Cinchona*. 11, 12 Capsules of *Anagallis*. 13, 14 Capsules of *Eucalyptus*. 15, 16 Siliques of *Brassica*. 8, 10, 11 enlarged; the rest natural size. (After Baillon.)

Like the follicle, the *Legume* or *Pod* arises from a single carpel, but on ripening it splits down *both* sutures completely to the base into two valves, which at the moment of dehiscence become rolled up spirally. This type of fruit is extremely common in the Leguminosæ. As examples may be mentioned *Lotus corniculatus* (fig. 325³) and the Senna (*Cassia angustifolia*, fig. 325⁴).

Dry dehiscent fruits, the product of two or more carpels, are termed *capsules* in the restricted sense. We may distinguish several types of capsules: (1) such as split into valves from the apex, as in the Birthwort (*Aristolochia*, fig. 325⁵), Rue (*Ruta*, fig. 325⁶) and Violet (*Viola*, fig. 325⁷); (2) such as open by means of teeth restricted to the apex, as in Caryophyllaceæ; (3) such as split longitudinally down the side-walls, the actual cavities of the fruit opening, as in the Wood Sorrel (*Oxalis*, fig. 325⁸); (4) such as produce several large apertures by the folding back of teeth, as in the Snapdragon (*Antirrhinum*, fig. 325⁹); and (5) such as form numerous



Fig. 326.—Achenes provided with a plume or pappus.

¹ Fruit of Valerian (*Valeriana officinalis*). ² The same in longitudinal section. ³ Fruit of the Artichoke (*Cynara Scolymus*). (After Baillon.)

small pores by the shrivelling of restricted areas, as in the Poppy (*Papaver*). The capsules of the Cinchona-tree (*Cinchona*, fig. 325¹⁰) split into two valves, which remain attached at the apex, separating at the base only; whilst many capsules dehisce transversely, a lid being removed, as in the Pimpernel (*Anagallis*, figs. 325¹¹ and 325¹²) and *Eucalyptus* (figs. 325¹³ and 325¹⁴).

A special form of capsule, known as the *Siliqua*, is characteristic of most Crucifers. It is usually described as consisting of two carpels, the exposed walls of which come away, leaving a framework (the *replum*) to which the seeds are attached. Stretched upon this framework is the membrane which formed the ("false") partition of the ovary. This class of fruit is well shown in Honesty (*Lunaria*) and in the Cabbage (*Brassica oleracea*, figs. 325¹⁵ and 325¹⁶). According to the terminology given at p. 75 (4), the two valves which come away correspond to the two outer non-ovule-bearing carpels, whilst the ribs which remain are the two inner ovuliferous carpels.

Though, in a great number of Angiosperms, the various floral-leaves disarticulate and fall away after pollination and fertilization, this is not universally the case: in a considerable number some of them remain behind, undergo various changes, and form an outside investment or appendage to the fruit which plays an important part in the dispersal or preservation of the seeds. The same is true of the bracts

and bracteoles, the leafy structures which are present in the immediate vicinity of the flowers, though not actually included in them. We may distinguish, perhaps, amongst these accessory structures of the fruit, between such as arise from portions of the perianth on the one hand, and such as are formed from bracts and bracteoles on the other. The enumeration of these structures here, however, must be distinctly limited to a few of the more commonly occurring.

A curious form of fruit obtains in the Mulberry (*Morus*). The female flowers



Fig. 327.—The Hornbeam (*Carpinus Betulus*) in fruit.

in this tree are arranged in little catkin-like clusters. Each flower consists of an ovary inclosed in an inconspicuous four-leaved perianth. From each ovary a tiny nut arises; but the ripe fruit resembles a succulent berry rather than a collection of nuts. This is due to the fact that after fertilization, whilst the ovaries are developing into nuts, their perianths become distended and fleshy, altogether concealing the ovaries. Without a knowledge of the mode of development, the perianth might now be readily mistaken for the true fruit-wall (pericarp), and the nut for the seed. In several species of Trefoil (e.g. *Trifolium agrarium*, *badianum*, *spadiceum*) the papilionaceous corolla is yellow. After fertilization this turns brown, dries up and forms a flying-arrangement for the small fruit within (cf. figs. 442^{1, 2, 3, 4, 5}).

It very frequently happens that the *Calyx* is retained as an accessory to the

fruit. In the Winter Cherry (*Physalis Alkekengi*), a solanaceous plant often cultivated in gardens, the calyx, originally small and green, becomes much inflated during ripening and forms a bright red bladder inclosing the actual berry; in the Henbane (*Hyoscyamus*), belonging to the same family, the calyx tightly incloses the capsular fruit, its periphery forming a characteristic funnel around the top. In Labiatae the calyx persists as a short tube, or as a bell or pitcher, at the base of which the actual fruit is found. In the Water Chestnut (*Trapa natans*, cf. vol. i. p. 607, fig. 144³) the four segments of the calyx become hardened and persist as four spines arranged cross-wise around the fruit. In many Valerians, Composites, and Scabiousses, the calyx persists, growing, as the fruit ripens, into a radiating crown

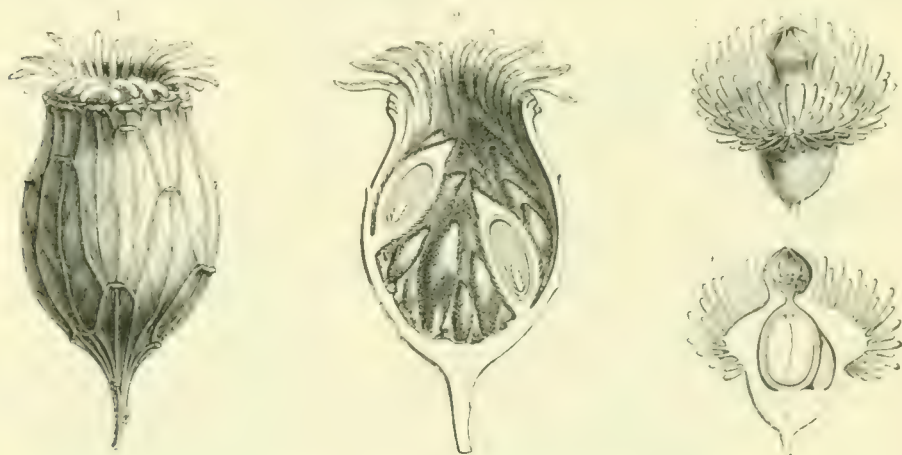


Fig. 328.—Fruits with persistent receptacles.

¹ The Carolina Allspice (*Calycanthus*). ² Longitudinal section of the same. ³ Fruit of *Agrimonia*. ⁴ Longitudinal section of the same. (After Baillon.)

of bristles or feathery hairs. This crown, known as a *Pappus*, serves the achene as a parachute (cf. figs. 326^{1, 2, 3} and fig. 447).

Amongst the Amentaceæ, trees whose flowers are for the most part destitute of perianth, the *bracts* and *bract-like scales* associated with the flowers often play a prominent part in the fruit. In the Grasses also the same feature is noticeable. In these latter the actual grain is very frequently closely enwrapped by one of the glumes, so tightly indeed, that they easily escape observation, as in Barley, Oats, and many others. The greatest variety of fruit-investment is met with in the Cupuliferæ and allied Amentaceæ, which include the Hornbeam, Hop-hornbeam, Beech, Hazel, and several other well-known trees. The actual fruit in all these is a nut, but inclosed in a peculiar involucre-like sheath (the *cupule*) derived from bract-like scales external to the flowers. In the Oak (*Quercus*) the cupule is cup-like (figs. 329¹ and 329²); in the Beech (*Fagus*) it completely envelops the paired triangular nuts, and is spiny outside, at ripening it bursts into four valves like a capsule; in the Chestnut (*Castanea*) it is extremely prickly, and, as in the Beech, bursts into valves (fig. 339⁴); in the Hazel (*Corylus*) it forms a lacinated, leathery envelope to the nuts (fig. 235, p. 147), whilst in the Hornbeam (*Carpinus*, fig. 327)

it has the form of a three-lobed open scale, to the base of which the ribbed nut is attached. Finally, in the Hop-hornbeam (*Ostrya*, fig. 437⁶) it forms a loose papery envelope.

The *Receptacle* of the flower is not infrequently a conspicuous feature in connection with the fruit. This is well shown in the Carolina Allspice, in Roses, and in Pomaceæ. In the Carolina Allspice (*Calycanthus*, figs. 328¹ and 328²) an excavated pitcher-like receptacle, invested on the outside with scales, incloses the achenes: in the Rose there is a similar inclosure, here smooth and fleshy, and bearing a five-leaved calyx above, this constitutes the hip. In the Apple, Pear, Quince, and other Pomaceæ, the receptacle forms an extremely succulent mass, in which the actual

fruit is imbedded, and with which it is entirely fused (e.g. Quince, *Cydonia*, fig. 330²). In the Strawberry (*Fragaria*), on the other hand, the fleshy receptacle is convex, and bears the little achenes scattered over its surface. Not always, however, is the receptacle fleshy; thus, in the Agrimony (*Agrimonia Eupatoria*, figs. 328³

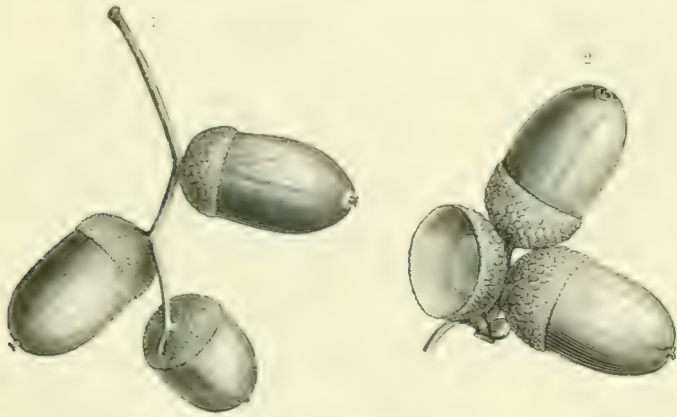


Fig. 329.—Fruits with Cupules

¹ *Quercus pedunculata*.

² *Quercus sessiliflora*.

and 328⁴) it forms a dry and woody inclosure for the one or two achenes, and is provided with numerous stiff hooked bristles on its periphery.

Much less frequently does the *flower-stalk* (pedicel) take a share in the fruit formation. This is so, however, in Anacardiaceæ, in some Rhamnaceæ, and in a few other groups. Thus, for instance, in the tree which produces Cashew-nuts (*Anacardium occidentale*, fig. 330¹), the upper portion of the pedicel swells up into a fleshy pear-like structure; on its summit is perched the kidney-shaped nut with its inclosed seed. In *Hovenia dulcis* (allied to the Buckthorn) a similar arrangement prevails, the flower-stalks are swollen, and contain a sweet red pulp appreciated by the Chinese and Japanese. To these instances may be added the Fig (*Ficus*, cf. figs. 240¹⁰ and 240¹¹, p. 157), in which the whole receptacle of the inflorescence is excavated, urn-wise, and becomes very succulent on ripening. The little grains inside, commonly taken for seeds, are in reality the actual fruits or nuts, each of which contains a seed. As a final instance may be mentioned the polygonaceous *Brunnichia africana* from west tropical Africa; in this case the flower-stalk becomes winged down either side, from its point of insertion up to the nut at its apex. It thus serves as a distributing organ for the fruit.

In many plants whose flowers are clustered very close together it often happens

that the fruits of the several flowers as they increase in size become more or less fused together; or the axis which bears them, or other associated parts, become fleshy forming a succulent matrix for the individual fruits. Such a mass of fruits is termed a *collective fruit*. Good examples of this are the Mulberry (*Morus*), the Pine-apple (*Ananassa sativa*), Piperaceæ, e.g. Betel Pepper (*Piper Belle*, fig. 331¹); and Arto-carpeæ, e.g. the Bread-fruit (*Artocarpus incisa*, fig. 332) and Jack-fruit (*Artocarpus integrifolia*). With these collective fruits may be contrasted the clustered crowded

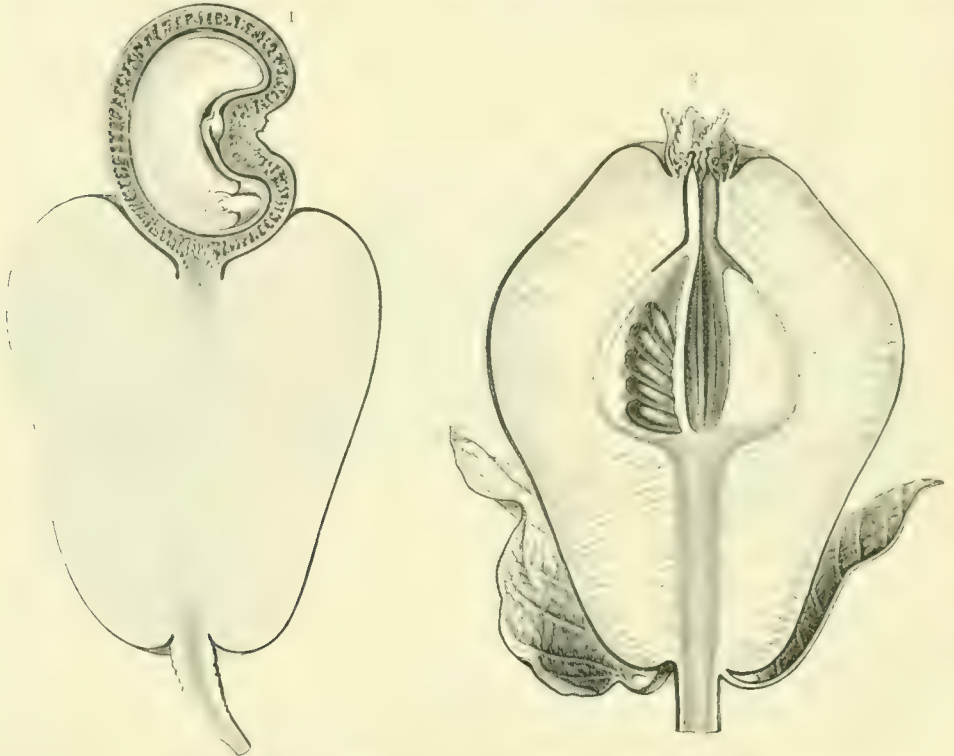


Fig. 330.—Fruits in whose structure the receptacle and pedicel take a share.

¹ Longitudinal section of the fruit of the Cashew-nut Tree (*Anacardium occidentale*). ² Longitudinal section through a Quince (*Cydonia*). (After Baillon.)

carpels produced from *single flowers* (*aggregate fruits*), such as the Raspberry (*Rubus Idæus*), *Calycanthus*, Rose, &c., already described, also many Anonaceæ, as, for instance, the West-Indian Sour-sop (*Anona muricata*, fig. 331⁴), the Sweet-sop (*Anona squamosa*, figs. 331² and 331³) and Custard-apple (*Anona reticulata*). The terminology that has grown up around the types of fruit described in this paragraph is extremely confusing and slovenly. We propose to call the compound fruit arising from a number of crowded flowers a *collective fruit*, that from the carpels of a single flower an *aggregate fruit*. An altogether peculiar fruit is that of the Lotus Lily (*Nelumbium speciosum*, cf. figs. 333 and 334). Here the receptacle is enlarged into a huge top-shaped structure in the middle of the flower (fig. 334¹); the upper surface of this top is like a honey-comb, and in each "cell", a carpel is sunk as in a socket

(fig. 334²). When the fruit is ripe and dry, these carpels form hard, woody achenes which rattle in their loose sockets like teeth in the jawbone of a skull.

Our descriptions of the fruit and its various forms and modifications relate, so far, solely to the Angiosperms. In the *Gymnosperms*, however, several essential differences are to be noted. The account of their methods of fertilization (pp. 418–420) was left at that stage at which the male sexual cell had fused with the egg-cell. The nucleus of the fertilized egg now moves down to the base (away from the

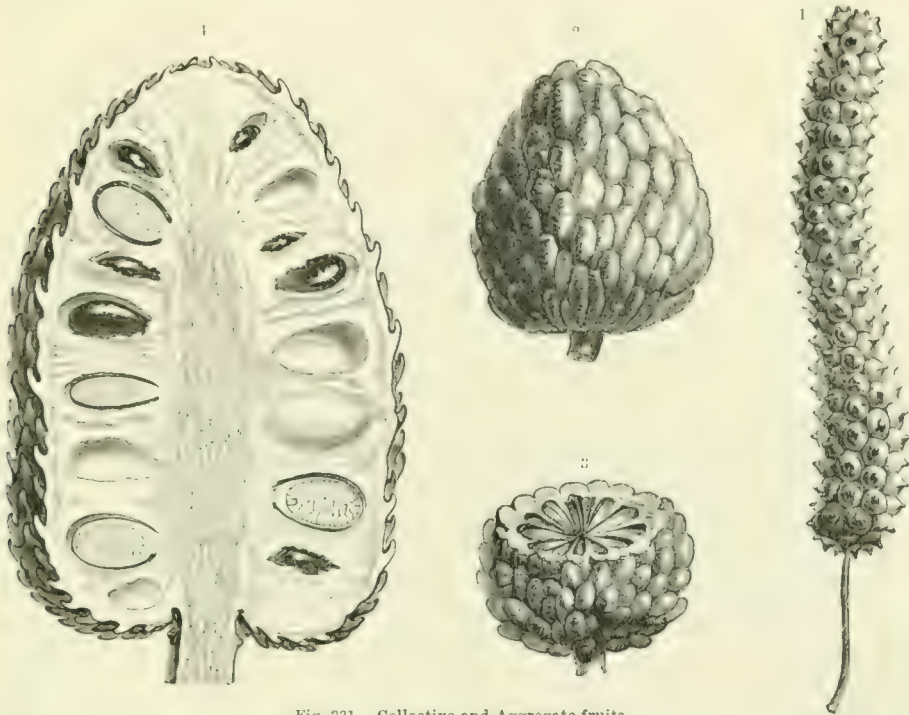


Fig. 331.—Collective and Aggregate fruits.

¹ Collective fruit of Betel Pepper (*Piper Bette*). ² Aggregate fruit of Sweet-sop (*Anona squamosa*) formed by fusion of the carpels of a single flower. ³ Transverse section of the same. ⁴ Longitudinal section of the aggregate fruit of the Sour-sop (*Anona muricata*) produced in the same way. (After Baillon.)

micropyle) of the egg-cell and divides several times, each product of its division becoming enveloped in protoplasm and ultimately in a cell-wall. In the Gnetales which many Botanists regard as more nearly allied to the Angiosperms than either of the other two families of Gymnosperms (*Coniferae* and *Cycadaceae*), there arise in this way from 2–8 daughter-nuclei around each of which protoplasm aggregates, and a cell-membrane is formed (*cf.* fig. 315², p. 415). Between each of these cells there is no connection: each grows out into a tube which penetrates the wall of the egg-cell and pushes its way down into the reserve-food (endosperm) below. From the tip of the tube a small cell, the embryonal cell, is cut off and from this cell by further division and growth an embryo is produced, which is nourished by the food-material. Of the many embryos which are inaugurated, one only comes to maturity, and is found in the ripe seed.

In the Silver Fir, Spruce Fir, Pine, and other Conifers, comprised under the family Abietineæ, the nucleus of the egg-cell divides into four at the base of the egg-cell, and here four little cells are produced, arranged like a rosette at that end. Each of these is divided into three stories, and the four cells forming the middle story elongate, diverge, and grow down into the endosperm, carrying the little embryonal cells at their tips. The four cells of the upper story remain attached to the residue of the egg-cell, and serve as a fulcrum for the elongating tubes—the suspensors. As in the Gnetales, the embryonal cells become modified into embryos,

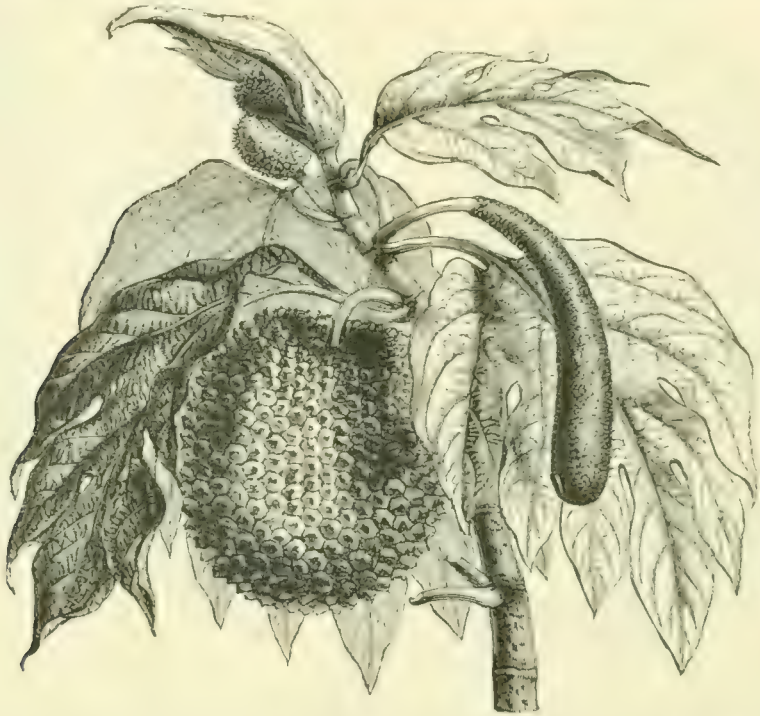


Fig. 332.—Branch of the Bread-fruit Tree (*Artocarpus incisa*) showing a male inflorescence (sausage-shaped, to the right), a female inflorescence (globular, near the apex) and a collective fruit (to the left). (After Baillon.)

but ultimately only one of them prevails, and, growing at the expense of the food-material, is a conspicuous object in the ripe seed (fig. 335⁶). A portion of the endosperm remains as a mantle around the embryo, and is only absorbed at germination.

In the Juniper, Arbor Vitæ (*Thuja*), Cypress, and other Conifers belonging to the family Cupressineæ, each egg-cell, after fertilization, gives rise to but a single embryo (though there are exceptions to this rule). Otherwise the events are not very different from those occurring in the Abietineæ.

The *Integument* of the ovule in Gymnosperms forms the seed-envelope (or testa), as in Angiosperms. The *Micropyle* becomes closed up, and the whole testa very hard. In the Pines, Firs, &c. (Abietineæ), the micropyle points *away from* the free margin of the open scale which bears the ovules (fig. 335⁷), *i.e.* towards the axis of

the cone; in the Cypress and other Cupressineæ, on the other hand, *towards* the free margin of the scale (figs. 337^{3, 4, 6}), and away from the axis of the cone.

In several species, as in the Stone Pine (*Pinus Pineæ*) and the Arolla Pine (*Pinus Cembra*), the seed-coat attains a thickness of $1\frac{1}{2}$ to 2 millimetres, so that the seed resembles a nut in appearance. Both these species, indeed, serve as an



Fig. 333.—The Lotus Lily (*Nelumbium speciosum*). (From a photograph.)

article of diet, being eaten like nuts. The seeds of Pines and Fir-trees are provided with a one-sided wing (cf. figs. 335^{3, 4, 5}) which plays an important part in their dispersal by wind. In the Maidenhair Tree (*Ginkgo biloba*) the integument of the seed becomes succulent and coloured a bright orange, so that the seed in a way resembles a drupe (cf. fig. 337⁷). In *Cycas revoluta*, also, the integument becomes red and fleshy (cf. fig. 208⁷, p. 74)

The ovules of both Abietineæ and Cupressineæ are inserted upon scales of varying form, the insertion of which on the axis of the cone may be broad or narrow (*cf.* figs. 335^{7, 8, 9} and 337^{3, 4, 6}). These scales form an important constituent of the ripe cone, and are known as the *ovuliferous scales*. In not a few cases, as in the Silver Fir (*Abies pectinata*, figs. 335^{1, 2, 3, 4}) and Larch (*Larix*, figs. 335⁸ and 337¹), there exists a second scale, the *bract scale*, beneath each ovuliferous scale, and subtending the same. In the Pine, also, both scales are present, though in the ripe cone there are no signs of the bract-scales at the exterior owing to the fact that they become entirely overgrown and embedded between the big ovuliferous scales.

In the Abietineæ the scales of the cones are inserted in a continuous spiral (*cf.* fig. 335¹, and vol. i. p. 403, fig. 101), whilst in Cupressineæ the scales are inserted in whorls of 2 or 3 scales each (*cf.* figs. 336^{6, 7} and 337^{3, 5}). In both, the margins of

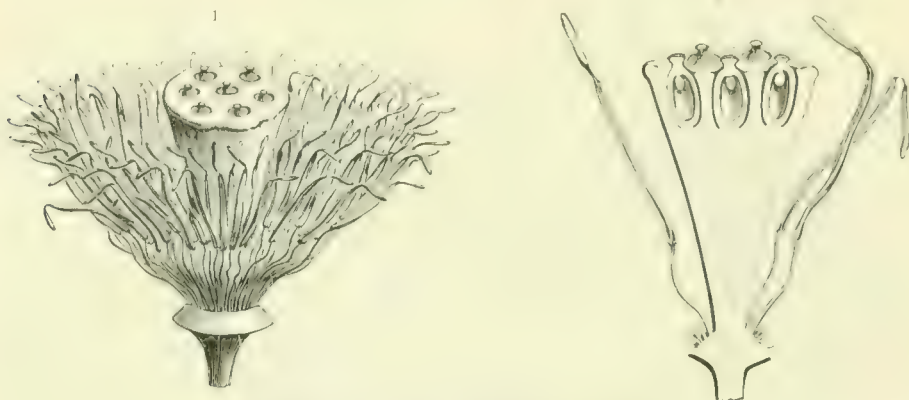


Fig. 334.—The Lotus Lily (*Nelumbium speciosum*).

¹ Flower from which the perianth-leaves have been removed; expanded receptacle in centre. ² Longitudinal section through the top-shaped enlargement of the receptacle, showing three carpels embedded in their sockets. (After Baillon.)

the scales overlap, and the seeds are ripened in the slit-like chinks between them (*cf.* 336⁶ and 337⁵). The whole assemblage of scales constitutes an aggregate fruit, and is known as a *cone*. The scales may be hard and woody, when we have a woody cone (335¹ and 337^{1, 2, 5}); or they may be succulent, giving a fleshy cone. In such fleshy cones very few of the whorls are succulent, the central axis is very short, and the whole structure has much the appearance of a berry, as in the Juniper (*Juniperus communis*, figs. 336⁷ and 336⁸).

The section of Gymnosperms known as the Taxineæ do not produce cones. Their seeds arise alone or in pairs at the ends of special short branches, or upon the surface of small fruit-scales. The plum-like seeds of the Maidenhair Tree (*Ginkgo biloba*) are arranged in pairs at the ends of axes which resemble cherry-stalks (see fig. 337⁷). The seeds of the Yew (*Taxus baccata*) occur at the tips of little scale-bearing shoots, and when ripe are almost completely enveloped in a sweet, fleshy, crimson tissue (see figs. 336^{1, 4, 5}). This fleshy inclosure, which arises as a circular cushion from the place of insertion of the ovule, is not of the nature of a carpel, it

is an aril. In *Podocarpus*, also, is developed a peculiar structure of the same kind.

In Cycads the seeds are borne upon carpels arranged in cones, and have a woody integument. In some cases they correspond in position to metamorphosed lobes of a carpel (*cf.* fig. 208⁷, p. 74), and have the outer layer of their integument developed as a succulent coat. In the Gnetaceæ, the seed at maturity is inclosed

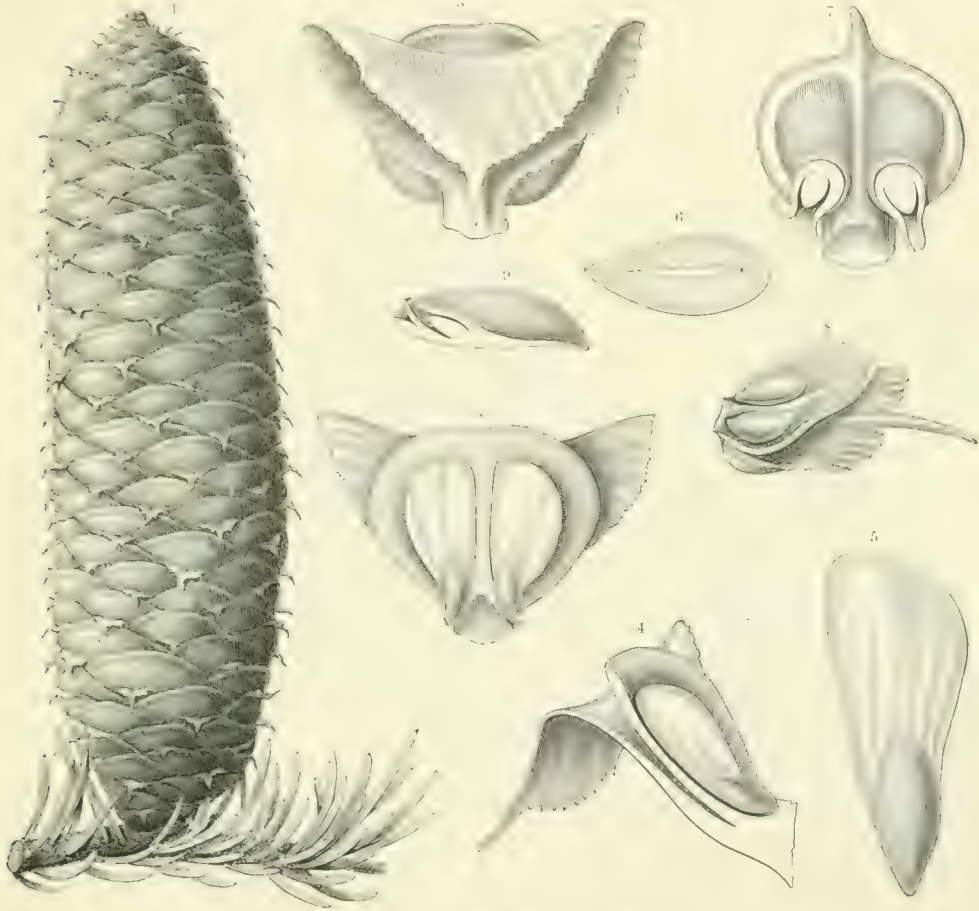


Fig. 335.—Fruit and Seed of Conifera.

¹ Cone of the Silver Fir (*Abies pectinata*). ² Bract scale and ovuliferous scale of the same seen from the outside (the bract scale is pointed). ³ Ovuliferous scale of same seen from above, showing the two winged seeds, and the bract scale behind. ⁴ Longitudinal section of bract and ovuliferous scales, showing a seed inserted upon the latter. ⁵ A winged seed of the same. ⁶ Longitudinal section of the seed. ⁷ Ovuliferous scale of the Scotch Pine (*Pinus sylvestris*) seen from above; it bears two ovules. ⁸ Single ovuliferous scale of Larch (*Larix europæa*) showing two ovules on its surface and bract scale (with bristle) below it. ⁹ Longitudinal section of the ovuliferous scale of the Larch. ¹ nat. size; the other figs. enlarged.

in a fleshy "perianth" in *Ephedra*; in *Welwitschia* cone-like collective fruits are produced; finally, in *Gnetum* leaf-structures around the seed unite to form cup-like receptacles for the seeds.

From the brief observations on the manner of fructification of Gymnosperms, it will be seen that their methods are very various, and that, in all cases, they differ from those of Angiosperms. They agree in the common object of producing a

vigorous embryo, and in providing it with adequate safeguards against unfavourable external conditions, and with means of dispersal, when the time comes for the seed to be detached from the parent plant and to take up an independent existence.

Whilst still attached to the parent plant, the embryo needs *protection* against the *ravages of animals*, and against *unfavourable climatic conditions*. Means of protection against the former are provided sometimes on the seed-coat, in other cases on the wall of the ovary; or they may be on other structures associated with the flower, or upon the flowering axis itself. These defensive arrangements fall into several groups. First of all, there are thorns, prickles, and spinous bristles, met

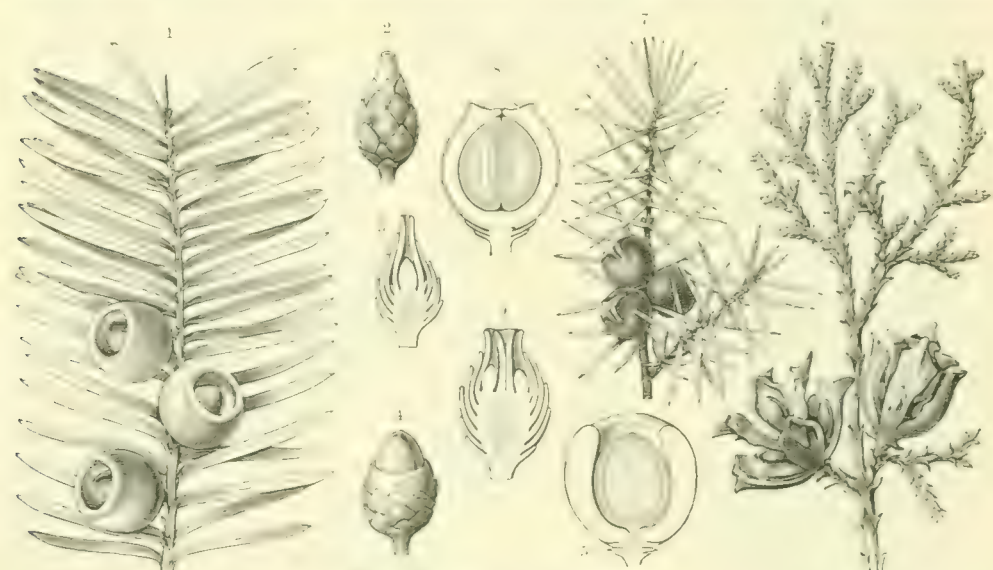


Fig. 336.—Fruits and Seeds of Coniferae.

¹ Branch of Yew (*Taxus baccata*) with ripe seeds, each inclosed in its aril. ² Tip of ovule of same projecting from between the scales of the little fertile shoot. ³ Longitudinal section of the same. ⁴ Young seed of the same only partly inclosed in its aril. ⁵ Longitudinal section of the ripe seed of the same, showing the aril. ⁶ Branch of the Arbor Vitæ (*Thuja orientalis*) showing female flowers and ripe, burst cones. ⁷ Branch of Juniper (*Juniperus communis*) showing berry-like cones. ⁸ Longitudinal section of one of these cones. ⁹ Female flower of Juniper. 1, 6, and 7 nat. size; the other figs. enlarged.

with especially on the ovary and immediate envelopes of the fruit. The capsule of the Thorn-apple (*Datura Stramonium*), that of the Anatto (*Bixa Orellana*, see fig. 338), the long 3-valved fruits of *Schrankia* (see fig. 339²), the pods of the Russian Liquorice Plant (*Glycyrrhiza echinata*), the persistent calyx of a steppe-plant, *Archieu cornuta*, and the cupule of the Chestnut (*Castanea vulgaris*, see fig. 339¹) may serve as examples. Several Pines, of which the North American *Pinus serotina* is a type, have cones the scales of which are produced into sharp spines (see fig. 337²), so that the seeds are inaccessible to animals till such time as the scales separate and the winged seeds are committed to the wind. Of interest in this connection are certain Crucifers (*Tetractium quadricorne*, *Matthiola bicornis*, *M. tricuspidata*, fig. 339³) in which, at the end of the fruit just below the scar of the style, 2, 3, or 4 stiff spines are formed, which make these fruits unaccept-

able morsels for animals. A less common condition, and one deserving of special mention, occurs in several *Mimosas* belonging to the immediate alliance of the Sensitive Plant (e.g. *Mimosa pudica*, *M. polycarpa*, *M. hispida*); of these the last-named may serve as type (see fig. 339¹). The pods here are densely crowded together, and their dorsal and ventral sutures form a strong framework bearing a double row of short spines. These spines hinder all animals from interfering with

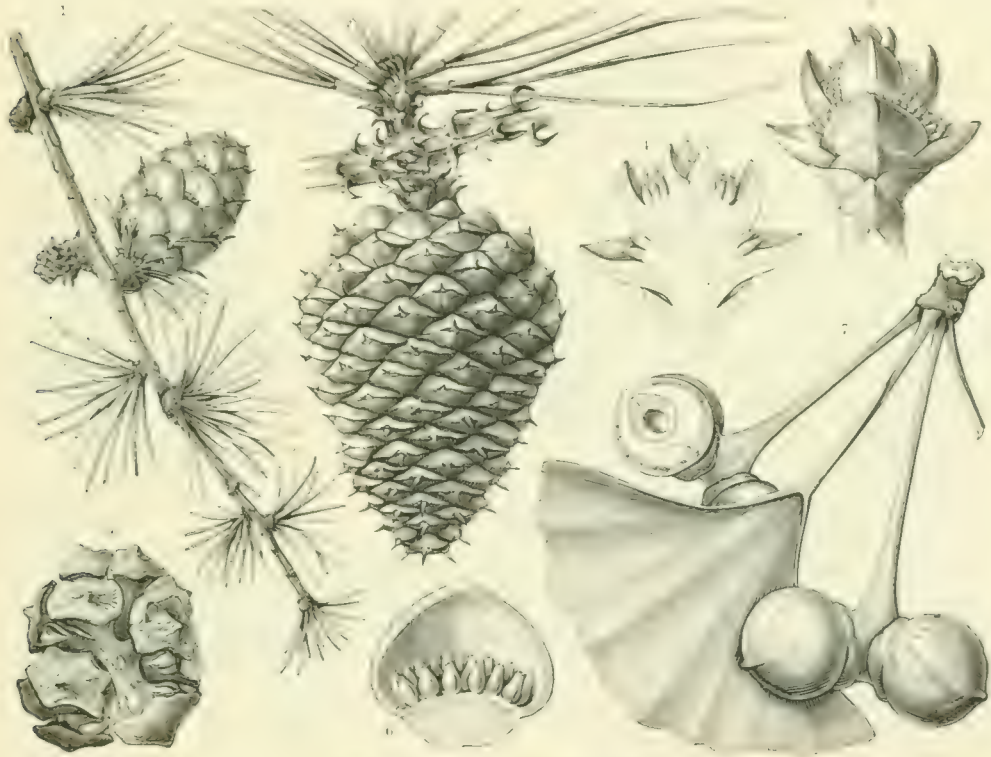


Fig. 337.—Coniferous Fruits and Seeds.

¹ Branch of the Larch (*Larix Europæa*) with ripe cone. ² Branch of *Pinus serotina* with ripe cone. ³ Female flower of the Cypress. ⁴ Longitudinal section of the same. ⁵ Ripe cone of the Cypress (*Cupressus sempervirens*). ⁶ Single carpel of the Cypress with numerous ovules. ⁷ Branch of *Ginkgo biloba* with unripe fruit. 1, 2, 5, 7 natural size. The other figures enlarged.

the fruits. As the seeds ripen, the valves fall away from their spiny framework, and are, with their contained seeds, dispersed by the wind. As a rule, the valves break up at this time into one-seeded segments (fig. 339¹), and being very light in proportion to their area, are carried considerable distances.

In the instances just enumerated the protection is provided only up to the time that the seeds are ripe. With the severance of the seeds from the parent plant the protective function of the spines is at an end. The spinose investment as a rule remains upon the plant, and only rarely, as in the winged fruit of *Centrolobium robustum* (see fig. 339⁵), does the thorny ovary wall (pericarp) become detached with its contained seed. Under these circumstances the spines may play a further

part, either by serving as a mechanism of dispersal, or by fixing the seed in the germinating bed.

In the case of plants with succulent fleshy fruits, the seeds of which are distributed by birds, it would be extremely disadvantageous for the fruits to be provided with spines or prickles when ripe. In point of fact, when such structures are present they often disarticulate and fall away as the fruits ripen, so that birds may have unhindered access to them. The fruits of the leguminous *Mucuna*



Fig. 333.—Protection of ripening seeds against animals.

The Anatto plant (*Bixa Orellana*) with flowers and fruit. Three of the fruits have opened showing the seeds (After Baillon)

pruriens are clad during their ripening period with a felt-work of serrated bristles, which contain an irritating fluid. These bristles cause an intolerable itching, or even an eruption of the skin, and, so long as they remain on the fruit, effectively guard it from animals. But as the seeds ripen, and the fruit becomes pulpy, these bristles fall away (so it is stated), and animals are no longer repulsed, but devour the pulp, and so disperse the seeds.

The well-known Hips of Roses which ripen in the autumn, do not fall away from the plant, but remain attached. The seeds are contained in

hard and tiny nut-like fruits, which are inclosed in the fleshy and excavated receptacle. They are destined to be distributed by blackbirds, jackdaws, and other birds, which devour the hips for the nutriment contained in the fleshy investment; the little nuts, however, pass out undigested in the droppings in some place more or less distant from the Rose-bush. Whilst these birds, attracted by the coloured fruits, are welcome guests, the case is quite the reverse as regards mice and other little rodents; they gnaw the nuts, and devour their contents, the seeds. But the Rose-hips are well-protected against these animals. The stems and branches, up which they must climb to reach the fruits, are provided with sharp prickles with downwardly-directed points, which give complete immunity against these animals. I have repeatedly, in the late autumn, when the mice desert the fields and take up their winter-

quarters in the abode of man, strewed the ground in my garden with Rose-hips of an evening. Invariably, next morning, I found that they had been gnawed and demolished by mice, whilst those remaining *in situ* on the plants were untouched. The fruits of several dwarf Palms are similarly defended against the attacks of animals, by zones of spines upon the stem, prickles upon the floral investments, &c. The berries of several shrubby Solanaceæ (e.g. *Solanum sodomæum*, and *S. sisymbriifolium*) gain a like protection, as do those of the Blackberry, from numerous prickles which clothe the stem and even the fruit-stalk and calyx. In

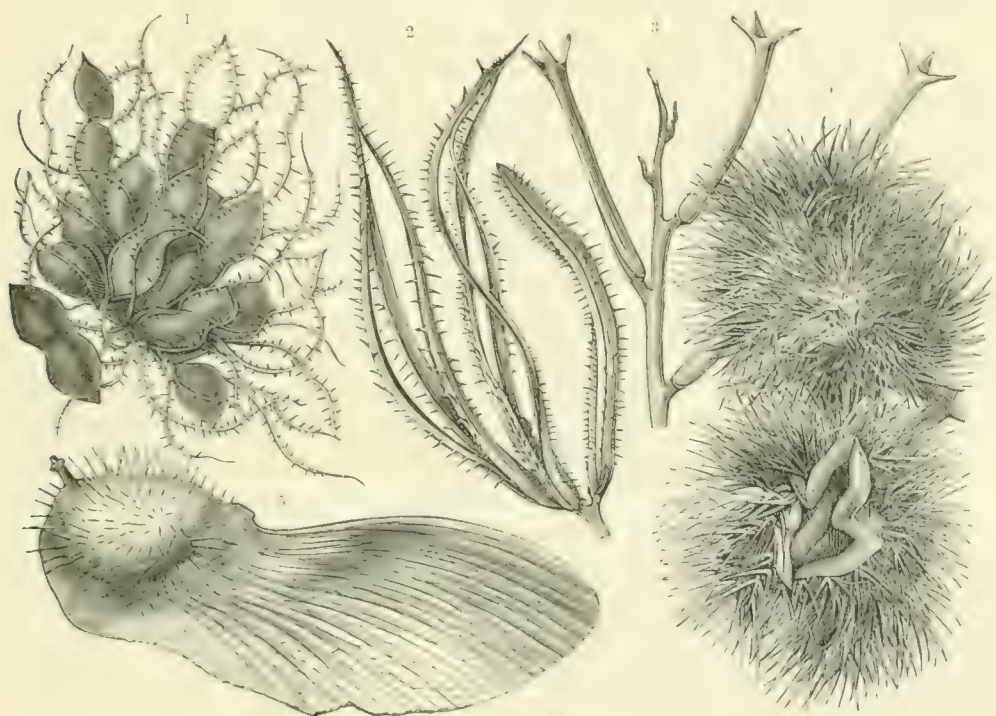


Fig. 339.—Protection of ripening seeds against the attack of animals.

1 *Mimosa hispida*. 2 *Schrankia*. 3 *Matthiola tricuspidata*. 4 *Castanea vulgaris*. 5 *Centrolobium robustum*.

several members of the Gorse genus, *Ulex Gallii*, *micranthus*, and *nanus*, the pods are borne upon branches which bristle with spines. The spines project beyond the pods, and their sharp points being directed downwards, mice are prevented from climbing up and working havoc.

Other animals besides these rodents, such as caterpillars, snails, earwigs, centipedes, and the like, have to be warded off. Some caterpillars find the green ovaries acceptable as food, others the seeds themselves. Still, as we have seen, it is of direct advantage to several Caryophyllaceæ, Leguminosæ, and species of *Yucca*, that a portion of the seeds should fall to the lot of insect-larvæ (*cf.* pp. 153–161). It may be repeated here that prickles and spines, the points of which are directed upwards, serve to protect the foliage against browsing animals (*cf.* vol. i. p. 432). In the above-mentioned case of the Gorse, the spines towards the tips of the

branches keep browsing animals away, whilst those inserted lower down, which are directed earthwards, prevent mice from climbing up the plant.

A peculiar protective contrivance has been observed on the calyx of several Labiates, e.g. *Thymus*, *Calamintha*, *Ballota*. The corolla falls away after fertilization, but the calyx persists, forming a sheathing envelope for the 4 nutlets. For the better protection of these nutlets the mouth of this cup-like envelope is closed by the development of a crown of hairs, which is impenetrable to small, seed-devouring animals. A further use of these envelopes in seed-dispersal will be alluded to in another place.

In other cases fruits are protected against unwelcome guests, not by spiny structures, but by the elongation of their stalks during ripening, rendering them inaccessible. Thus it would be a difficult feat for a mouse to reach the pendent pods of the Pea (*Pisum*), or those of the Vetches (*Vicia dumetorum*, *V. pisiformis*, *V. sylvatica*). Should by any chance a pod be accessible to these animals, by some other route, it is as good as lost, as the nutritious seeds of these plants are much sought after by them. Cherries also, on their long stalks, no doubt derive considerable immunity from earwigs, centipedes, &c., as those which fall to the ground are speedily attacked and devoured.

In the case of seeds whose dispersal depends on the attraction of animals by sweet, fleshy pericarps, these tissues are the reverse of appetizing before they are ripe; not until the seeds are ready to be separated from the parent plant do fruits of this kind become attractive. It is only necessary to cite as instances unripe Cherries, Plums, Apples, and Grapes. It was stated on a previous occasion (vol. i. p. 462), when dealing with chemical changes occurring in plant-tissues, that the fleshy parts of fruits are rendered disagreeable to animals before they are ripe by the presence of bitter or poisonous glucosides, &c. Later on these substances are altered, perhaps under the influence of the acids, which are present in large quantities in unripe fruits, and their place taken by sugars and other harmless materials; thus, what is at first unattractive, and even repulsive, becomes, on ripening, a nutritious food, much sought after by animals, which, at the same time, unconsciously disperse the contained seeds. In this connection the Walnut (*Juglans regia*) is very instructive. Until the seed contained in the "nut" (here really the stone of a drupaceous fruit) is ripe, the latter is surrounded by a fleshy investment rich in tannin. It is not known at this stage that the "nuts" are ever interfered with by nut-crackers or other animals. But on the ripening of the seed the fleshy envelope splits, and the "nut" becomes accessible.

In other cases it is not by acids or bitter stuffs that the seeds are protected, but by strong-scented resinous or sticky substances, which are contained in the cells and passages of the fruit. Thus, in the scales of the cone of the Arolla Pine (*Pinus Cembra*) quantities of resin are present until the seeds are ripe. If the cones be cut with a knife this resin escapes, and can only be removed from the blade with the utmost difficulty. Were a nut-cracker to peck the scales at this stage to obtain the young seeds, its beak would get all besmirched with the resin. It

is easy to observe at Zermatt and Arolla in the Pennine Alps, where this Pine grows, that the nut-crackers attack only the fully-ripened side of even almost ripe cones. As the cone ripens the seeds become easily accessible, but with their manner of dispersal we shall deal in a later section of this work. Here we are concerned only with the fact that many ovaries and fruit-envelopes render their contents undesirable to animals by sticky secretions or disagreeable scents. The pods of several Leguminosæ, *e.g.* species of *Adenocarpus* (*A. decorticans*, *A. Hispanicus*, &c.), are invested both on their flat sides and round the edge with short-stalked, sticky, brown glands, which are to be regarded as a protective arrangement for the young pod. The same obtains in the Hemp (*Cannabis sativa*), though here it is not the ovary but the scales immediately about it which are sticky and strongly odorous. So also in the Hop (*Humulus Lupulus*), the fruits are invested in scales bearing glands which play a like part. Even the ubiquitous sparrow leaves the fruits of these two plants alone during the period of ripening.

Of not less importance to the young embryo is protection against *injurious climatic influences*. Among these, undue moisture and dryness are the chief; and it is to be expected that due provision against them should be made on behalf of the young plant whilst it remains on the parent. Seeds contained in berries, drupes, and indehiscent fruits, as well as those which, produced in capsules, are dispersed at the moment of fruit-dehiscence, hardly come under consideration here, as the opportunities for hurt by weather are relatively small. But in the case of dehiscent fruits which open by means of valves, teeth, or pores, and in which the seeds are retained for some time after the opening of the fruit before they are scattered, provision must be made against the entrance of rain into the cavity of the fruit, which might injure the seeds. This class of danger is averted by the fact that the various valves, teeth, &c., which guard the apertures of the fruits, are very hygroscopic and close in humid weather; or, what is equivalent to this, they only open in dry weather, especially under the influence of drying winds. To make this remarkable contrivance intelligible we must briefly describe the arrangements for seed-dispersal obtaining in capsules of the kind. Capsules opening by valves, teeth, &c., are usually inserted on long stalks, or, if sessile, the axis from which they arise possesses considerable length. These stalks are fairly stiff, and oscillating to and fro in gusts of wind the contained seeds are shaken out, usually as the capsule springs back after the blast. In the case, for instance, of the beaker-like capsules of the Nottingham Catchfly (*Silene nutans*, fig. 340⁵) the seeds cannot fall out of their own accord, the opening being directed upwards; but as soon as the wind sets the long stalk in vibration they are jerked out. For this mode of scattering of the seeds it is essential that the apertures of the fruit should be directed upwards. Indeed, in the great majority of cases of this class, this is their position. In this Catchfly at the time of flowering the flower-stalks are pendent (see figs. 238 and 239, pp. 154 and 155), but, as the fruit ripens, the fruit-stalk becomes erect; the same thing is well shown in the Martagon Lily. On the other hand, when the fruit-stalk bends down after flowering, as in the Bellflower (*Campanula*,

fig. 340¹) and in the Winter Green (*Pyrola*, fig. 340⁶), the holes and slits are not formed at the apex of the fruit, which is directed downwards, but at its base, close to the insertion of the stalk. This position of the apertures would render the inside of the capsule liable to wetting from rain, &c., and the contained seeds to injury therefrom, were it not for the fact the openings are closed when this danger threatens. The wall of the capsule is very hygroscopic, and the slits and valves quickly close in damp weather. In fig. 340 several examples of this opening and



Fig. 340.—Protection of seeds against wet.

¹ Capsules of *Campanula rapunculoides* in dry, 1' in wet weather. ² Capsule of *Lychnis diurna* in dry, 2' in wet weather.

³ Capsules of *Linaria Macedonica* in dry, 3' in wet weather. ⁴ Capsules of *Cerastium macrocarpum* in dry, 4' in wet weather. ⁵ Capsules of *Silene nutans* in dry, 5' in wet weather. ⁶ Capsules of *Pyrola chlorantha* in dry, 6' in wet weather.

⁷ Capsules of *Gymnadenia Conopsea* in dry, 7' in wet weather. ⁸ Capsule of *Pinguicula vulgaris* in dry, 8' in wet weather.

closing are represented. In the already mentioned capsule of the Catchfly (fig. 340⁵) the aperture at the summit is guarded by a number of divergent teeth; the same is true in the case of those of various species of Toadflax (e.g. *Linaria Macedonica*, fig. 340³). In *Cerastium macrocarpum* (fig. 340⁴) the opening is directed laterally, and in the Campion (*Lychnis diurna*, fig. 340²) the capsule is erect with revolute teeth. In the Bellflower (e.g. *Campanula rapunculoides*, fig. 340¹) small, circumscribed portions of the wall near the base fold back as valves, giving rise to as many apertures; in the Winter Greens (e.g. *Pyrola chlorantha*, fig. 340⁶) a number

of slits arise near the base, while in the Butterwort (*Pinguicula vulgaris*, fig. 340⁶) the fruit splits into two valves. How all these capsules behave is shown in the portion of the illustration with the shaded background (figs. 340¹ to 340⁵). Closure is so complete that the entrance of moisture into the capsules is impossible, and the seeds have absolute immunity from premature wetting. Even in the case of capsules with lateral slits, where there is a possibility of moisture entering, the same arrangement prevails, as is well illustrated in the Fragrant Orchis (*Gymnadenia Conopsea*, cf. figs. 340⁷ and 340⁸).

Of capsules with openings directed downwards there are but few, and in these the dispersal of the seeds is not accomplished quite in the same manner as in those just described. In the Funkias (*Funkia ovata*, *Sieboldi*, *subcordata*, &c.) the pendent capsules open by three valves at their depressed tips, and concurrently some of the seeds are shot out into the air—often to some little distance. Those which remain in the capsule after the sudden opening are not, as one might expect, deposited in a heap on the ground close by, but, being attached to the valves by delicate strings, and having a flattened form, offer considerable surface to the wind, which ultimately loosens them and bears them far away. The fact should be emphasized that in many cases fruits only open under the influence of dry winds, and that the same wind which promotes their dehiscence at the same moment scatters the seeds. This is very well shown by the Scotch Pine (*Pinus sylvestris*). Its cones only separate their scales in the afternoon when the air is driest and a wind is blowing. When the conditions for this are favourable one hears quite a series of noises in the tree-top, caused by the separating of the scales, and at the same time the winged seeds go spinning through the air. The scales protect the seeds in this case against wetting, and indeed against other dangers as well. It should be remembered that any protective arrangement is but rarely directed solely against one particular source of danger. An envelope may protect the embryo at one time against the wet, at another against excessive desiccation: sometimes the same envelope may also ward off attacks from undesired guests of the animal world.

Developments on fruits whose chief function is the protection of the seeds against *desiccation* are, on the whole, scarce. In certain portions of Australia the whole vegetation enters upon a sort of summer sleep: during this period no rain falls and the surface of the earth is hardly ever wetted with dew: such a dryness of the air and of the soil prevails that plants are compelled to suspend operations for a while. It has been already explained how the foliage is protected against drying up (cf. vol. i. p. 296); but the embryo also, which has arisen within the ovule during the period of vegetative activity, has to be preserved during this period. This is achieved by the massive development of the ovary wall, which in this respect exceeds anything met with in the Floras of other regions of the globe. The seeds of the Wooden Pear (*Xylomelum pygmaforme*, see fig. 325² p. 431) are inclosed in a strong pericarp, the wall of which attains a diameter of 2 centimetres, and can resist the greatest dryness for very long periods. So also is it with the seeds of the Australian species of *Banksia* and *Eucalyptus* (see figs. 324 and 325^{10, 11} pp. 429

and 431), the walls of their capsules being exceedingly thick and strong. In not a few Steppe-plants the seeds within are protected by the nature of the inclosing pericarp during the hot, rainless summer season. Remarkable amongst them are the big Umbelliferous genera *Prangos* and *Cachrys*, the schizocarps of which are protected by a thick spongy wall not unlike elder-pith in nature. Preserved within these walls against desiccation, the embryo secures this further advantage, that from the relative largeness and lightness of the fruits they are readily dispersed by the wind over the Steppe.

In dry, dehiscent fruits protection against unfavourable climatic conditions is extended only so long as the seeds remain attached to the parent plant: in achenes, nuts, and schizocarps it lasts longer, however. For in the latter classes of fruit the pericarp accompanies the seed after severance, protecting and aiding it during its passage, and often assisting it at germination. All those developments of the seed-coat, met with in the cases in which the seeds themselves are liberated, are replaced, in these non-dehiscent fruits, by the pericarp or other associated portion—calyx, bracts, and the like. These structures are fashioned so as at once to preserve the seed on its journey, be it by air or water, and to attach it to its germinating-bed by various irregularities of surface—pits, furrows, warts, or even sticky excretions. Further, it is important that arrangements be provided so that the young plant should have access to water at certain spots on the fruit wall, and that on germination it should be able to push out its young rootlet without undue effort, as, for instance, in the Water-chestnut and Bulrush (*cf.* vol. i. p. 607, figs. 144³, 4, 11, 12, 13).

The stage of development at which the embryo is detached from the parent plant is not the same in all cases. In the Maidenhair Tree (*Gingko biloba*) the embryo is but slightly differentiated at the time when the plum-like seed falls. The egg-cell has been already fertilized, and the enveloping tissues of the seed have matured, but the differentiation of the embryo is postponed till after the seed has fallen. So, too, in Orchids and in many parasitic and saprophytic plants, such as *Cuscuta*, *Orobanche*, *Monotropa*, and Balanophoræ, the embryo, at the moment of severance of the seed, is of the most rudimentary character. But in the majority of Phanerogams the embryo shows a differentiation into plumule, and radicle, and cotyledons. In *Ceratophyllum* the plumule has already slightly elongated and exhibits a number of little leaves, and in *Nelumbium* the leaves show a differentiation into blade and petiole. In the Mangrove Tree (*Rhizophora Mangle*, see fig. 341¹) the embryo attains to a very considerable degree of development whilst still attached to the parent plant. Its root penetrates the wall of the ovary (fig. 341²) and ultimately attains a length of 30–50 cm. and a thickness of 1–5 cm. and a weight of some 80 grams. Finally, the young plant breaks away from its sucker-like cotyledon and falls into the mud below, where it speedily unfolds a pair of green foliage-leaves (*cf.* vol. i. p. 604). Thus, in the Mangrove Tree, it is not the seed but the embryo which is detached from the parent plant. Comparing the *Gingko* to an oviparous animal, the Mangrove might be regarded as viviparous.

The envelopes which surround the embryo at the moment of detachment vary

enormously from plant to plant. The seed of the terrestrial Orchid *Gymnadenia*



Fig. 341.—Mangrove Tree (*Rhizophora Mangle*).

¹ Branch with flowers and fruits (reduced). ² Single fruit, the apex of which is being penetrated by the radicle of the embryo. (After Baillon.)

Conopsea measures 1 mm. in length and weighs .008 gram: that of the Cocoa-nut Palm 11–14 cm. and weighs 800–1100 grams. The Wind Bent-grass (*Apera spica-*

venti) has a grain 1·2 mm. long, ·3 mm. broad, and weighs ·05 grm.; the fruit of the Seychelles Palm (*Lodoicea Sechellarum*) measures 32 cm. by 18–25 cm. by 22 cm., and weighs 4200–4800 grams. The largest fruits are produced by the Cucurbitaceæ; in a suitable soil Gourds attain a diameter of half a metre, whilst fruits of the Melon-pumpkin (*Cucurbita maxima*) have a greatest diameter of over a metre, and a weight of 75 to 100 kilograms. The fruits of the Bottle-gourd (*Lagenaria*) attain under favourable circumstances a diameter of 30 cm. and a length of a metre and a half.

3. CHANGE IN REPRODUCTIVE METHODS.

Fruits replaced by Offshoots.—Parthenogenesis.—Heteromorphism and Alternation of Generations.

FRUITS REPLACED BY OFFSHOOTS.

By *Annual Plants* are understood such as germinate, grow, and conclude their flowering and fruiting within the limits of a single year, and after the ripening of their seeds die away. The activity of these plants is concentrated on the production of a large amount of seed; it is worthy of note that autogamy is frequently met with amongst them, followed by good results. They produce just so many foliage-leaves as are necessary to provide the materials for their flowers and fruits, and reserve-substances for their seeds. With the production of seed, the leaves, stems, and roots perish without forming vegetative buds or offshoots, so that these plants are represented for several months by their seed only. Their rejuvenescence can only occur under favourable climatic conditions where an unimpeded germination is allowed these seeds, and when no interference in the process of development is imposed by men or animals. If the weather be unfavourable in the situations where the plants have established themselves, if the summer be a cold one, so that fruit cannot be ripened, they do not perish at the end of the first year, but prolong their existence till another year by means of offshoots, becoming, for the time being, perennial plants. We may put it, in a manner of speaking, that when the danger of extinction threatens, fruit-production is replaced by offshoots; instead of fruits, tubers, buds, or other shoots are produced, and not infrequently these structures arise in the position usually occupied by fruits. Among the Crassulaceæ there are several annual species (*Sedum annuum*, *glaucum*, &c.) which normally die away so soon as their seeds have ripened and been dispersed. But when it happens from any cause—as by the premature on-coming of winter—that these processes are interfered with, little rosettes of leaves arise from the base of the stem in close proximity to the root; these are detached, and, as offshoots, continue the life of the plant into another season. Similar phenomena are observed in many other herbs whose flowers or fruit are destroyed by frost. Indeed by experiment these statements can be readily verified. Members of various families (*Poa annua*, *Senecio nebro-*

densis, *S. vulgaris*, *Ajuga Chamaepitys*, *Herniaria glabra*, *Viola tricolor*, *Cardamine hirsuta*, *Medicago lupulina*), normally annual, are transformed into perennial plants when grown in my alpine experimental garden on the Blaser in Tyrol (Gschnitzthal), at a height of 2200 metres, there being insufficient warmth there for them to produce good seed.

Interference with fruit-production due, in inhospitable situations, to an unfavourable climate, can be artificially brought about by the removal of the flowers from a plant as they appear. Annual plants pruned in this way produce shoots and offshoots which would otherwise have remained undeveloped. These remain living till next year, and if the same treatment be continued indefinitely, a plant, otherwise annual or biennial, becomes perennial. Upon this fact depends the gardening feat of producing little Mignonette trees. Normally the seeds of this plant germinate in a sandy and humous soil, and the plants arising perish in the autumn after flowering and ripening their fruit; but if the inflorescences be carefully pinched off, the stem doesn't die down but produces lateral shoots with the object of developing new flowers. If these flowers be removed year after year, gradually a little tree is formed, with woody stem and branches; and if ultimately it be left alone will cover itself with hundreds of sweet-scented flower-spikes. That a much increased production of leafy shoots and offshoots can be stimulated in perennial plants by this kind of pruning has long been known; by its aid many modes of propagation, as practised in horticulture and agriculture upon cultivated plants, are obtained.

It sometimes happens in nature that a failure of flowers is due to the plants being overshadowed. That is to say, many plants growing in shady places either do not produce flowers or their flower-buds do not open and cannot ripen fruit. Such plants produce offshoots from the lower portion of their stem in the form of leafy shoots, runners, &c., if they are able to do so, and this in a very marked degree; in other words, the more flowering and fruit-production is hindered by shading, the more is a development of offshoots promoted. The Willow-herb (*Epilobium angustifolium*) develops its beautiful flowers only in sunny situations, accessible to hive- and humble-bees. The more intense the sunlight, the more vividly are the flowers coloured. Should trees grow up and densely overshadow the Willow-herbs, the flower-buds atrophy before opening and fall away from the axis as small withered structures. Whilst the richly-flowering plants form only short offshoots, these shaded plants produce long, subterranean runners, which seek to penetrate to a distance, out of the circle of shade.

Another remarkable phenomenon in the growth of perennial plants, which flower and fruit copiously under favourable climatic conditions, is that in inhospitable situations, where this is restricted, they propagate themselves very readily by means of offshoots. A Composite, *Nardosmia frigida*, allied to the Butter-bur, is widely distributed over the Arctic regions. Only towards its southern limits does it produce flower and fruit; further north flowers are never met with upon it, but, instead, it propagates itself far and wide by means of

offshoots. Similar in its behaviour is another Composite, the alpine *Adenostyles Cacialia*. It blossoms and fruits in sub-alpine forests even up to the tree limit, but in high alpine regions, above 2200 metres in altitude, it never flowers, but forms offshoots, and in this way fills little depressions on alpine slopes with its vigorous foliage. The terrestrial form of *Polygonum amphibium* occurs in a little bog close to my country house in the Gschnitzthal in the Tyrol at a height of 1200 metres. For twenty-eight years I have examined this bog every year without ever finding a ripe fruit upon these plants. But it propagates itself with rare luxuriance by means of offshoots and forms a broad girdle around the bog. These plants, *Nardosmia frigida*, *Adenostyles Cacialia*, and *Polygonum amphibium*, grown in a more favourable climate, produce good seed, but their vegetative methods of propagation are so restricted that one might almost suppose them to be different species of plants.

Instances in which flowers are replaced by offshoots or bulbils in the inflorescence may be mentioned in connection with the above. *Polygonum viviparum* and *bulbiferum*, *Saxifraga cernua*, *nivalis*, and *stellaris*, *Juncus alpinus* and *supinus*, and the Grasses *Aira alpina*, *Festuca alpina* and *rupicaprina*, *Poa alpina* and *cenisia* occur, it is true, with normally developed flowers and fruits, but in alpine, and especially in arctic regions, where these plants have their headquarters, one very frequently finds purely vegetative buds or bulbils, which become detached from the parent plant and give rise to new individuals, in place of flowers and fruit. In the *Polygonums* mentioned little bulbils replace a portion of the flowers. *Saxifraga cernua* usually produces a single terminal flower at the end of its inflorescence, the lateral flowers being replaced by little tufts of bud-like offshoots on short stalks (see fig. 342³). These buds, when they fall off, are either still closed (fig. 342⁵), or their thick, fleshy, outer scales are already parted, exposing a little green foliage-leaf. On the ground they soon produce roots and grow into new plants (see figs. 342⁹ and 342⁷). In *Saxifraga nivalis* little shoots are formed in place of flowers, each bearing a tuft-like rosette of minute leaves (fig. 342¹). These rosettes are readily separable, and producing roots from their abbreviated axes, give rise to new plants. So also in the *Juncuses* and Grasses mentioned, little shoots replace the fruits and come away from the inflorescence. These shoots are produced in *Poa alpina* (see fig. 342⁸) and in most of the other Grasses mentioned, in the following manner. The axis of each spikelet, after producing several glumes at its base, forms green leaves above—as it were a grass-plant in miniature (see figs. 342⁹ and 342¹⁰). Later, these disarticulate, take root, and grow into new plants. More rarely do shoots arise laterally on the axis, in the axils of subtending scales: when this is the case they fall away in the usual manner. The earlier Botanists termed all such Grasses, and indeed all plants which produce bulbils in their inflorescences, *viviparous*, the idea being, that in all of them the seeds germinated precociously whilst still attached to the parent. This view was probably suggested by the common experience of agriculturalists that Rye, Oats, and other cereals sometimes “sprout”, i.e. that when the spikes are continually wetted by rain about

the time of harvest, and the haulm laid flat on the ground, the embryos begin to develop whilst the grain is still in the ear. This premature germination, however, is quite independent of the parent plant, which has given up all its food-materials, and is already dead; the grains, held between the glumes mechanically, are no longer in vital connection with the plant which gave them origin. Their germination between the damp husks is similar to what would occur between pieces of moist blotting-paper. But in these so-called "viviparous plants" the phenomenon



Fig. 342.—Bulbils replacing flowers and fruits.

¹ *Saxifraga nivalis* with rosettes of little green leaves instead of flowers (natural size). ² Two of these rosettes, enlarged; one of these has become detached from its stalk. ³ *Saxifraga cernua* (natural size). ⁴ A cluster of bulbils of this plant. ^{5, 6, 7} Bulbils of same in various stages of development. ⁸ *Poa alpina* with bulbils replacing its flowers (natural size). ⁹ A portion of the inflorescence (enlarged). ¹⁰ A miniature grass-plant developed between the glumes of a spikelet of *Poa alpina* (enlarged).

is quite different from this "sprouting" of cereals. In them no flowers or seeds are formed, consequently there can be no germination of seeds still united to the parent plant. The detached structures, formerly regarded as germinated seedlings, are in reality little, leafy shoots which have been produced instead of flowers and fruits.

The plants which we have just been discussing are essentially forms living in high alpine and arctic regions, that is to say, in regions in which they have but some two to four brief months in the year in which to complete their vital processes. In the majority of plants growing under such inhospitable conditions,

the flowers for the following summer are already developed in miniature the preceding autumn, so that on the melting of the snow and the termination of winter the flowers can be at once expanded. When such plants can avail themselves of the warmth of the whole summer they are able to ripen fruit and seed. But it is otherwise with those which produce their flowers on a leafy axis, and which must first form an under-structure on which they can be produced; with these, before flowers can be unfolded, a considerable interval of time must elapse. Their blossoming is delayed, and the ripening of their seed takes place quite at the end of the period of vegetation. There is thus always the danger of early frosts or of the winter-covering of snow intervening before the seeds can be ripened and dispersed. It is in just such plants that preservation and propagation are ensured by a development of bulbils; these structures are more speedily produced than seeds, nor do they require so much warmth; further, they are not so liable to injury from premature advent of winter as are developing fruits. The above-mentioned Polygonums, Saxifrages, Rushes, and Grasses are amongst those which flower relatively late, and are liable, in unfavourable seasons, to a destruction of their seeds. The very frequent substitution in them of vegetative for sexual reproduction would seem to be undoubtedly correlated with this liability of seed to fail. And in not a few steppe-plants the substitution of offshoots for flowers is probably connected with the fact that with them, also, the season is not always long enough for the formation of stem, flowers, and fruit.

It has been previously pointed out that a great many aquatic plants, with roots fixed in the mud and stems and foliage floating in the water, raise their flowers above the surface and avail themselves of the wind and of flying insects for pollination and fertilization. For such plants fluctuations in the level of water must be of considerable moment, and it may well be that if the surface is raised for any length of time, flowering and fruiting are hampered, and, in many cases, rendered impossible. Many marsh and water plants possess, indeed, the capacity of stretching to the surface, the stem continually elongating as the level is raised, until the flowers can be expanded above the surface. But this growth in length has its limits, and it not infrequently happens that, even after an extraordinary elongation of stem and flower-stalk, the surface of the water is not attained. And these flowers in most cases cannot be fertilized under water; if already formed, the flower-buds do not open, but atrophy and fall off without producing fruits. In the little meres of the Black Forest, *Littorella lacustris*, a plant allied to the Plantain, grows; but it only flowers and fruits in very dry years, when the expanse of water is much contracted and the bottom is in large part laid bare. But this is not very often; ten years may pass without the conditions favourable to the flowering and fruiting of *Littorella* obtaining. During the whole of this time the plant must remain barren were it not for the fact that off-shoots, which take root in the mud, are produced instead of fruits. Thus it is able to maintain and propagate itself. Several Pondweeds and Water-crowfoots (*Potamogeton* and *Ranunculus*) behave

like *Littorella*, and it would appear that the capacity to propagate by offshoots, so common in aquatic plants, is connected with the impediment to flowering so often presented by a high water-level. *Cymodocea antarctica*, a submerged aquatic plant, which grows in great luxuriance on some parts of the coast of Australia, flowers so rarely that its peculiarly formed bulbils were for a long time regarded as its flowers. Nor has every Botanist seen the flowers and fruits of the Duckweed (*Lemna*); whilst the renowned American Water-weed, *Elodea canadensis*, which has been such an obstacle to navigation in canals, &c., but seldom flowers, and owes its very remarkable propagation and distribution, not to fruits, but to a quick and plentiful production of offshoots.

A dearth of water, also, like a too ample supply, can render fertilization impossible and promote the propagation and distribution of some plants by offshoots to a remarkable degree. In Ferns and Mosses the spermatozooids reach the archegonia, swimming in the water which accumulates on or about the sexual generation of these plants (*cf.* pp. 65 and 68). In the great majority of cases, it is rain and dew which provide the capillary water which invests the plants, and in which the spermatozooids swim. And other conditions in the life of Ferns and Mosses besides fertilization depend on an adequate supply of water; their existence depends on a certain definite amount and on a certain annual duration of atmospheric precipitation. Mosses, and particularly Ferns, have but a restricted distribution in dry localities; or they may be entirely wanting. In humid regions, on the other hand, they attain to a luxuriant growth. The contrast in this respect is striking enough for illustration. Elvend Kuh, a mountain in the interior of Persia, rises to a height of some 3750 metres, and is the culminating point of a considerable plateau. The rainy season is limited to a period of two months, and a rich and well-marked steppe-flora covers the ground. Ferns are absent from an area some 5000 square kilometres in extent, whilst Mosses are only represented by a few species which propagate by means of thallidia, rarely maturing spore-capsules. In the hill country of the West Indies, particularly the Blue Mountains of Jamaica, the vapour condenses every morning, and in the course of the afternoon is precipitated as rain. Here are found some 500 Ferns, and large numbers of Mosses and Liverworts. The level or sloping ground, rocks, the forest floor and decaying tree-trunks, all are covered with Ferns of every shape and size; there are groves of Tree-ferns, the trunks of trees are invested right up to the crown with delicate, green fronds, whilst tiny representatives of the Filmy Ferns (*Hymenophyllaceæ*) have actually taken up their abode on the foliage-leaves themselves. Within a distance of a hundred paces the plant-collector can find fifty different sorts of Ferns, and as many Mosses.

And between the extremes we have described there are regions with an intermediate climate, of such a character, that although the fertilization of Ferns and Mosses is not perpetually prevented, still wet years are rare, and several years may elapse without the conditions being favourable for it. Such a region is the Hungarian plains, the fields and woods of which produce only two species of Ferns and

some dozen Mosses. The latter have almost entirely ceased developing fruits, and propagate themselves for the most part by thallidia, since these can be produced much more simply, and their production is independent of enduring drought.

Certain Ferns must be mentioned in this connection, on the prothallia of which offshoots arise instead of normal, sexually produced embryos. It is true that they form archegonia, but they are abortive, and propagation is asexual. The little Fern-plant arises not from the archegonium but from the tissue in its immediate neighbourhood; the archegonia remain closed, are not fertilized, turn brown, and die. This substitution may be observed in *Aspidium falcatum*, in a crested variety of *Nephrodium Filix-mas*, and in the variegated form of *Pteris Cretica*, frequently cultivated in greenhouses. On the prothallia of normal forms of *Nephrodium Filix-mas*, and on those of wild plants of *Pteris Cretica*, fertilization takes place in the usual way, so that it is possible that the substitution of offshoots for fruits is a result of the conditions of cultivation. To what causes exactly the phenomenon in question may be due, is, however, unknown.

As factors in promoting a substitution of offshoots for fruits amongst the Mosses, other climatic conditions exert considerable influence. But it would lead us too far were we to treat of all these in detail; only a few of the fifty or so examples from the European Moss-flora can be mentioned here. *Leucodon sciuroides*, a Moss which rarely fruits in Northern Europe, produces instead numerous leafy shoots (brood-bodies) which, becoming detached, readily root on a moist substratum (see figs. 196⁹ and 196¹⁰, p. 23). *Campylopus fragilis*, again, scarcely ever produces fruits in the Alps; it forms readily separable lateral branches, the leaves of which are carried away by the wind. Any of these leaves falling on a moist spot develops green filaments, upon which little buds arise, originating new leafy Moss-stems (see fig. 196¹¹, p. 23). The case of *Barbula fragilis* and *Timmia Norvegica*, growing in the Alps, is similar to that of *Campylopus*. Of several Mosses the fruits have never been seen; such are *Dicranodontium aristatum*, *Barbula papillosa*, *Grimmia torquata*, *Bryum concinnum*, and *B. Reyeri*. They are able to maintain themselves in spite of this by vegetative propagation.

In addition to the cases already enumerated, in which climatic conditions, excess or lack of water, &c., promote vegetative as opposed to sexual reproduction, numerous others are known in which peculiarities in the structure of the flowers cause the ovaries to abort, or make it necessary that a formation of offshoots should be initiated if the plants are to be maintained. In this connection certain hybrid Fuller's Thistles and Mulleins (*Cirsium* and *Verbascum*) must be noted. The plants in question are hybrids, that is to say, they are produced by crossing of different species. They flower early in the summer, and have ample time to ripen seed before the on-coming of winter, but in a number of these hybrids, owing to variations in the structure of the flowers and of the pollen, few or no seeds are ripened. On the other hand, just these very plants form aërial buds and subterranean offshoots very freely. *Cirsium purpureum*, a hybrid between

Cirsium heterophyllum and *spinosissimum*, and *Cirsium affine*, a hybrid between *C. heterophyllum* and *C. oleraceum*, are very abundant in many Alpine valleys, and one may find more examples of these hybrids than of their parents in many a meadow. Several of the Fuller's Thistle hybrids, the parents of which are biennial, become perennial by a production of lateral shoots from the leaf-axils at the base of the stem. Here also, as with climatic conditions, we find vegetative propagation replacing fruit-production.

There are also many species, of which it cannot be definitely asserted that they have arisen by hybridization in recent times, which fruit but seldom even when the climatic conditions are in every way favourable for this kind of reproduction. According to agriculturists, there are many kinds of Potato which flower only occasionally but do not ripen fruit, although the flowers and pollen-grains appear quite normal. It is just these Potatoes which are characterized by their rich production of tubers, fruit-formation being in them replaced by vegetative propagation.

That plants, with double flowers, the ovaries of which, under the influence of little insects (*Phytopus*), have undergone a deep-reaching transformation, should ripen no fruits is to be expected and has long been known, as also is the fact that these plants produce buds and offshoots freely. Of special note in this connection is a Bitter-cress (*Cardamine uliginosa*) often met with in damp meadows in the neighbourhood of Vienna, Salzburg, and Ried, growing wild with double flowers. On most of the plants, the fruits of which are abortive, those curious leaf-buds, represented in fig. 200⁴, p. 41, are to be found.

Again, with many species of plants, it may come to pass that the insects which should accomplish their pollination are now no longer prevalent in the region where the plants grow, or indeed have entirely deserted them. This category of plants obviously includes only such forms as are destitute of arrangements for promoting autogamy, in the case of cross-pollination not taking place. In a very considerable number of these plants, flowers and fruits are replaced by offshoots—offshoots of the most varied kinds, including aerial and subterranean tubers, bulbils, green leafy shoots, and, in rare cases, little bud-like structures, from each of which a thick, fleshy root arises in such a manner that the greater part of the offshoot consists of a root.

As all these varieties of offshoots will be dealt with in a later chapter devoted to the distribution of such structures by wind, animals, and special mechanisms, it must suffice to speak here of a very few cases. Growing in sunny spots, the yellow flowers of the Lesser Celandine (*Ranunculus Ficaria*) are occasionally visited by little pollen-eating beetles, by flies and bees; under these circumstances heads of fruit are ripened here and there from the flowers. But in shady places, beneath bushes, and on the dark forest floor, these insect-visits are much rarer, and almost all the flowers fail to ripen fruit. These shaded plants, however, develop little bulbous bodies in the axils of their upper foliage-leaves, which become detached on the withering of the shoot and give rise to new plants (see

fig. 343³). Those which ripen fruit, on the other hand, form no offshoots, or only very few. In the Coral-root (*Dentaria bulbifera*, see figs. 344¹ 2, 3, 4, 5) a similar state of affairs prevails. Pollination is accomplished only by insect-agency, and where insects fail no fruits are ripened. The plant grows sometimes near the sunny border of young Beech-plantations where insects are plentiful, and also in the forest of older growth in whose dusky glades bees and flies, humble-bees and butterflies are rarely met with. Those which grow in the better lighted, younger



Fig. 343.—Flowers and fruits replaced by tubers and bud-like offshoots.

¹ *Gagea Persica*. ² *Lycopodium Selago*. ³ *Ranunculus Ficaria*. ⁴ Bud-like offshoot from the leaf-axil of *Gagea Persica*.
⁵ Bud-like offshoot of *Lycopodium Selago*. ⁶ Tuber-like offshoot of *Ranunculus Ficaria*. 1, 2, 3 nat. size; 4, 5, 6 enlarged.

portion of the wood ripen their cruciferous capsules, but the others, in the deep gloom, are free of insects and blossom in vain. Their ovaries for the most part abort and fall away, and only occasionally do their fruits come to maturity (*cf.* fig. 344²). But in proportion as fruit-production is arrested, vegetative propagation by bulbils is promoted; large bulb-like buds are formed in the leaf-axils, which disarticulate as summer advances and the shoot begins to fade; they are detached by the wind as it sways the stems, and falling on the moist floor of the forest take root (fig. 344⁴) and give rise to subterranean rhizomes (fig. 344⁵). Some plants

occur in these shady spots which bear no flowers at all, and depend entirely on a production of these offshoots (*cf.* fig 344³).

There are two forms of Orange Lily indigenous to Europe. One (*Lilium croceum*), occurring especially in the Pyrenees and South of France, almost always ripens fruits and forms no bulbils in its leaf-axils. The other (*Lilium bulbiferum*),



Fig. 344.—Flowers and fruits replaced by bulbils. The Coral-root (*Dentaria bulbifera*).

¹ Inflorescence. ² Leafy shoot on which two fruits have ripened; bulbils in the axils of some of the leaves. ³ Leafy shoot whose inflorescence has atrophied; bulbils in the axils of all the leaves. ⁴ Detached bulbils forming roots. ⁵ Rhizome of *Dentaria bulbifera*.

found in the valleys of the Central and Northern Alps, hardly ever fruits, but is characterized by the bulbils it produces in the axils of its leaves; bulbils which disarticulate in autumn and are scattered by the wind. But there is no difference noticeable in the structure of the flowers in these two Orange Lilies, and it is difficult to explain their difference in mode of propagation, save on the assumption

that in the regions where *Lilium bulbiferum* grows those insects are wanting which should convey its pollen from flower to flower. As the Orange Lily possesses no arrangements for autogamy, no fruits are formed in the absence of insect-visits. It appears that this plant has lost the capacity for autogamy: at any rate if a stigma be pollinated with pollen from the same flower, on plants in a garden, no result follows. On the other hand, offshoots in the form of numerous bulbils are produced by *Lilium bulbiferum*, by means of which it is propagated and dispersed. In several valleys of the Central Alps it does not flower at all, and thus obviously depends entirely upon its bulbils for propagation.

Gagea Persica (fig. 343¹) a member of the Liliaceæ, repeats several of the peculiarities met with in the Orange Lilies. The stem of this little bulbous plant terminates in a flower which, in the absence of insect-visits, withers without setting fruit. Little buds arise in the axils of its filamentous foliage-leaves. With the atrophy of its fruits these grow into little bulbils (fig. 343¹); but if fruit be formed these buds for the most part atrophy. Nor must we omit to mention the ally of this plant, *Gagea Bohemica*, belonging to the flora of Central Europe. From its specific name, *Bohemica*, it might be supposed that it is solely met with in Bohemia; this is not so, it was first discovered there, but is distributed widely over Persia, Asia Minor, Southern Russia, and the Balkan Peninsula. Further west *Gagea Bohemica* occurs rather sparingly, in Bohemia and in the neighbourhood of Magdeburg—these occasional occurrences being no doubt a last lingering remnant of a Steppe-flora which at some former period extended to the Harz Mountains. We shall later have opportunity of explaining how this Steppe-flora has retreated eastwards and been replaced by other communities of plants; here we may mention that this retreat of the Steppe-flora was accompanied by a retreat of the Steppe-fauna. The Steppe-antelope, Steppe-marmot, Steppe-porcupine, rat-hare, &c., which existed in those times in Central Germany, have long forsaken this region, and we have good grounds for assuming that the insects of that period have also migrated. It is certainly remarkable that this Steppe-plant, *Gagea Bohemica*, the flowers of which are adapted to insect-pollination, and in which autogamy does not occur, should never ripen its fruit and seeds in these scattered localities of Bohemia and Germany. One can hardly help supposing that this abortion of fruits is due to the absence of those Steppe-insects which were formerly, in all probability, distributed also over Bohemia and Germany. Whatever be the explanation, it is a fact that these isolated western representatives have never been known to ripen fruit and seed. But instead, at the bases of the leaves, bulbils are formed which fall away and root, maintaining and propagating the species.

Equally instructive is the case of one of the Chickweeds, *Stellaria bulbosa*, now confined to a restricted area in Carniola and Croatia. It flourishes there in the deep, black humus of the forest floor, preferably on the banks of little water-courses, forming here and there dense, luxuriant masses. Its flowers unfold quite early in the spring; and although they are fairly conspicuous, standing up white from the green background, they are rarely visited by insects. The few flies which come to

them seem to be undesired guests; they promote no pollination, and fruits are not ripened. I have sought vainly for fruits in the neighbourhood of Laibach in Carniola where *Stellaria bulbosa* is very abundant; there were thousands of faded flowers, but never a fruit with ripened seeds. Its filamentous subterranean stems, on the other hand, bear innumerable white buds; and if one digs up a handful of the black woodland mould, it simply teems with these offshoots. The little streams in spate after a thunderstorm often wash away some of the humus from their banks, exposing and carrying away these little buds in the whirl of waters. Ultimately they are left somewhere, high and dry; and if the conditions are favourable, take root and establish themselves in these new localities. In this manner, at the present time, is *Stellaria bulbosa* propagated and distributed. We cannot suppose things have always been thus; we are driven to the conclusion that in this case, also, the plant, much restricted as to its distribution, is a fragment of a vanished flora. In the Karst district of Carniola and Croatia such fragments are not infrequent, and when one puts all the facts together one may well conclude that this flora has retreated or been driven back in a south-easterly direction at a period not very remote from our own. Accompanying these changes there may well have been changes in the distribution of the insect-fauna, and those insects which formerly visited the now rare *Stellaria bulbosa* of the Karst, and were of great importance to it, may have migrated eastwards or indeed have become extinct.

PARTHENOGENESIS.

At the commencement of the Nineteenth Century the attention of Botanists was directed to a certain aquatic plant, widely distributed in the Old World from Ireland to China, and from Finland to Northern Africa, and occurring very commonly on the Baltic littoral and its islands. This plant was *Chara crinita*, one of the Characeæ, which flourishes in brackish water near the sea, and here and there in salty, stagnant inland lakes. In whatever ditch or pool it takes up its abode it occurs in large quantities, and forms, like many of its allies, extensive and luxuriant masses. It is an annual plant, dying off in the autumn. Next spring young plants arise from the oogonia which have passed the winter on the muddy bottom—and so from year to year. *Chara crinita* is dioecious, that is to say, some plants bear oogonia only, others antheridia (*cf.* p. 62). Whilst in the generality of dioecious Characeæ the male and female plants grow in one another's immediate vicinity, in *Chara crinita* such a distribution is extremely rare. Hitherto, male plants have only been found at Courthezon, near Avignon, in the South of France; near Gurjew on the Caspian Sea; and at Salzburg, near Hermannstadt, in Siebenbürgen (Hungary). I have myself found plants bearing antheridia in some little salty pools near Soroksar, south of Buda-Pesth in Hungary. In the North of Germany on the shores of the Baltic, where *Chara crinita* is very abundant, a male plant has never been found. Nor have Botanists been wanting in their endeavours to find such, should any occur in this region. The Dassower See near

Lübeck, the neighbourhood of Warnemünde near Rostock, the two Jasmunder Boddens (inland branches of the sea), on the island of Rügen, and the Wanger Wieck near Stralsund, where *Chara crinita* is exceedingly plentiful, have been repeatedly searched for male plants but in vain. And the female plants also have been examined in case, perchance, an occasional antheridium might occur upon them, as in the monœcious species of *Chara*. Thus we may take it as established that in the Baltic region no antheridia and consequently no spermatozoids are developed. Nor was the attempt successful to explain the matter on the supposition that at the time of fruiting spermatozoids were brought by water-birds from Hungary, the Caspian, or the South of France. In the Baltic the egg-cells of *Chara crinita* remain unfertilized in their oogonia; the latter fall off in autumn and, without stimulus from any spermatozoid, germinate in the spring. We have here an instance of what Zoologists have termed *Parthenogenesis*. It has been demonstrated with certainty that new individuals arise from unfertilized eggs in the Spruce-gall Aphis (*Chermes*), in plant-lice (*Aphis*), and in many bees, wasps, &c. Also, in the Silk-worm Moth and in *Solenobia*, larvæ arise from unfertilized eggs and these pupæ give rise only to females. This is of interest in that from the unfertilized oogonia of *Chara crinita* only individuals with oogonia arise.

Cases similar to *Chara crinita* are thought to exist in several plants found in water or on moist substratums. In the genus *Syzygites* (now included in *Sporodinia*), a mould-like Fungus belonging to the Mucorini (*cf.* p. 54), the protoplasm in the conjugating branches forms the starting-point of new individuals without any actual fusion or conjugation taking place. So also in the Saprolegniaceæ it often happens that the egg-cells in the oogonia form new plants without being fertilized; probably renewed investigations will bring to light similar relations in many Peronosporæ, Siphonaceæ, &c.

Amongst the Mosses parthenogenesis does not seem to be so very rare. In them, as in Characeæ, fertilization is accomplished by means of water; the plants are wetted by rain and dew, and this moisture is held by capillarity in the chinks, &c., between the leaves. The fertilizing spermatozoids travel some distance, swimming through the water to reach the archegonia. This distance is not very great in many forms, and these ripen their fruits freely. But there are several species in which only male plants occur in one locality and female plants in another—it may be hundreds of miles away. Such species are *Paludella squarrosa*, which occurs in North Tyrol with antheridia, and in Bohemia with archegonia only; *Grimmia Hartmanni*, found in the Alps with antheridia, and in the Carpathians with archegonia. *Neckera Besseri*, *Aulacomnion turgidum*, *Bryum alpinum* and *B. Duvalii*, *Didymodon ruber*, *Barbula recurvifolia*, *Amphoridium Mougeotii*, *Mnium insigne*, *Pterogonium gracile*, *Hypnum rugosum*, and *Thuidium abietinum* are further examples of which we cannot treat here in detail. As it is impossible for the archegonium of a Moss in the Carpathians to be fertilized by a spermatozoid from an antheridial plant in the Alps, and as fruits are ripened nevertheless, though not very abundantly in truth, it may well be that these are

cases of parthenogenesis, cases, that is, of egg-cells which continue their development unfertilized.

Amongst Flowering Plants, also, cases are known in which ovules sometimes, without ever being fertilized, form embryos which grow up into healthy plants. An instructive example is the case of *Gnaphalium alpinum* (= *Antennaria alpina*), a perennial Composite nearly allied to both the common Cat's-foot (*Gnaphalium dioicum*) and *Gnaphalium carpaticum* of the Alps and Carpathians. This plant occurs in Scandinavia from Telemarken to Havosund (59° 52' to 71° north. lat.), and in Russia from Finland to the Kola Peninsula, also in Arctic Siberia, in Arctic America, in Labrador, Melville Peninsula and the whole Arctic Archipelago, in Greenland between the parallels 60° and 72° north lat., finally in Iceland. Thus it is distributed in a zone surrounding the North Pole, some 12° in breadth. It is absent from the mountains of Central and Southern Europe, and is not known to exist, for certain, on the mountains of Central Asia. In these northern latitudes *Gnaphalium alpinum* is exceedingly common, occurring abundantly in innumerable localities. But it is a remarkable fact that neither in Arctic America nor in Arctic Asia has a plant producing pollen ever been found. In the Scandinavian Flora once, in the year 1842, a pollen-bearing plant was alleged to have been discovered; but this has been discredited. A large number of Botanists, thoroughly familiar with the Scandinavian Flora, are unanimous in saying that they have never seen stamen-bearing flowers, and that ovaries only occur. I have myself obtained plants of *Gnaphalium alpinum* from the Dovrefjeld in Norway, and have flowered them in my garden. Every flower produced an ovary but no pollen, so that the possibility of pollination was excluded. A number of achenes ripened containing good seeds, and these, carefully cultivated, produced plants, in all respects similar to the parent form. When these young plants flowered the same phenomena occurred. Thus, one has good grounds for asserting that *Gnaphalium alpinum*, throughout the wide area of its distribution, is propagated parthenogenetically, and that its reproduction is not hindered by the absence of pollen-bearing plants.

Another plant, of which it has been long known that embryos arise in its unfertilized ovules, is a species of Dog's Mercury (*Mercurialis annua*, see fig. 345), one of the Euphorbiaceæ, widely distributed in fields and gardens, in hedge-backs and waste places, throughout Central Europe. Some individuals of this species produce staminal flowers only (fig. 345¹), others, female flowers only (fig. 345²). Its dust-like pollen is conveyed to the stigmas by currents of air, and the ovaries of the female flowers ripen seeds freely as the outcome of fertilization. But female plants have often been cultivated in pots by themselves, with the result that they also ripened seed, though smaller in amount than when there is access to pollen, as is the case with plants growing freely in the open. These results were much canvassed, and discredit thrown upon them by many. It was urged that the dust-like pollen might have come from afar, in the air, and have entered the conservatory in which the experiments were conducted; and again it was

pointed out that many female plants of *Mercurialis annua* bear here and there a male flower alongside the female ones. For the refutation of these objections fresh experiments were necessary in which every precaution should be exercised to eliminate sources of error. Such experiments should be conducted in some district in which for miles around the plant did not grow wild, so that the possibility of casual introduction of pollen might be excluded. Fulfilling this requirement is the Central Tyrol, from which both the annual and perennial species of Dog's Mercury are absent. Accordingly I repeated in my upland garden in the Tyrolese Gschnitzthal the cultural experiments originally carried out in 1833 by Ramisch at Prague. Every precaution was taken to avoid sources of error;



Fig. 345.—The Annual Dog's Mercury (*Mercurialis annua*).

1 With male flowers.

2 With female flowers.

and in particular were all plants destroyed which showed a tendency to produce male flowers, and the utmost vigilance kept lest an isolated male or hermaphrodite flower should make its appearance anywhere. At the time when the stigmas were ready to be pollinated there were no pollen-grains of this plant anywhere in the neighbourhood for miles around, so that the possibility of such a pollination was excluded. Nevertheless the ovaries set and fruit was ripened, and from the seeds young plants arose.

Another plant, also belonging to the Euphorbiaceæ, in which embryos arise in unfertilized ovules, is *Cælebogyne ilicifolia*. It was introduced into Europe from the bush of Eastern Australia in 1829, and is now in general cultivation as a hot-house plant in Botanic Gardens. The first specimen introduced bore only female flowers, and all the plants which have been raised from this specimen, and distributed over Europe, resemble it in this respect. Plants of *Cælebogyne* with male flowers are unknown in European conservatories. The possibility of such

occurring on the female plants (*cf.* p. 300) has not been ignored, but they have never been detected on the plants used for observations; consequently its own pollen has never had access to the stigmas of the plants in question. In spite of this, ripe seed has been obtained and new plants raised from it, which, in their turn, bore only female flowers. Nor do these new plants differ in any way from the plant originally introduced; this observation is of importance, as it might be suggested that they were hybrids, that the pollen of some other euphorbiaceous plant had reached the stigma, there produced pollen-tubes and fertilized the ovules of *Cœlebogyne*. But this is not so, otherwise the offspring would give some indication of such origin. And the plant itself gives indication that it is not fertilized by any pollen. If a plant of *Cœlebogyne* be kept apart where no pollen has access to it, it can be noticed that its stigmatic lobes remain quite fresh for a long time, even till the ovary begins to swell. Only later do they fade, when the seeds are well advanced. This observation is of value since in ordinary cases the stigmas fade very soon after pollination, and it is only unpollinated stigmas which retain their freshness (*cf.* p. 285). In view of these oft-confirmed results, from which all possible source of error has been eliminated, we may conclude that the ovules of *Cœlebogyne ilicifolia* are able to produce embryos without the co-operation of the male protoplasm.

We may now consider whether the instances just described can be regarded as cases of true fruit-formation. As the essence of fruit-formation is a union of ooplasm and spermatoplasm, or in other words, fruit-production must be preceded by fertilization, and as this condition is not fulfilled, these structures are not true fruits. In the absence of fertilization, we must regard these reproductive bodies as brood-bodies, or a special form of offshoot. As has been previously mentioned (p. 44), brood-bodies can arise from any portion of a thallus, from any portion of the stem, and from leaves of the most various kind. A brood-body can originate from the protoplast of a cell of a Lichen-thallus or of a Moss-leaf, from one in the root of an Ash-tree or in the stem of an Orange Lily, on the margin of an Orchid-leaf, or over the midrib of a Begonia-leaf; why not also from the protoplast in the oogonium of *Chara crinita*, or in the archegonium of a Moss, and in the ovules of *Gnaphalium alpinum*, *Mercurialis annua*, and *Cœlebogyne ilicifolia*? Experience shows that in the great majority of cases, both in the Cryptogams and in the Phanerogams, the young commencements of the fruits abort if the ooplasm be denied the spermatoplasm which should fertilize it; but it also shows in unmistakable manner that in a few plants the ooplasm does not die even in the absence of fertilization.

Without entering upon profitless speculations belonging to the domain of Nature-philosophy, we may discuss the question of the possible reasons for the curious behaviour of the "fruits" in these cases. And first of all it may be observed that all the plants exhibiting the phenomenon of parthenogenesis are dioecious. For such plants a crossing with other individuals is alone possible. But what occurs should a crossing in such plants be impeded from any cause? It

seems contrary to the economy of plants that the egg-cell, produced at great expense of energy, and in a sense the culmination of a plant's activity, should wither away unproductive. Plants with hermaphrodite flowers can, if denied crossing, resort to autogamy. But this is of course impossible with dioecious plants; instead of autogamy the formation of embryos in unfertilized oogonia and ovules is a possibility open to them, whereby their outlay of material and energy shall not be wasted. Dioecious plants, which are likewise annuals, are especially liable to the danger of extinction in the absence of pollen and consequent fruit-production; for them the death of the individual may connote the disappearance of the species. Against such possibilities many precautions exist amongst plants, notably the formation of offshoots or brood-bodies; the leafy shoots arising from these structures preserve the plant from such a contingency. In the same way we may regard the formation of brood-bodies in the ovules of dioecious plants as a means contrived to prevent the extinction of the species. The fact that brood-bodies are formed in the ovules of not a few dioecious plants to which pollen has not ready access, supports this view. There has been a specimen of the Californian bush, *Obione halimifolia* (an *Atriplex*, *Chenopodiaceæ*), for many years in the Vienna Botanic Garden. This plant is dioecious; the Vienna plant bears only female flowers, and pollen is not accessible within hundreds of miles. Its stigmas remain unpollinated, and its ovules unfertilized. But as the autumn draws in, the ovaries of this plant begin to swell, and the perianth which ensheaths the ovary expands, and what appear to be fruits are formed. But these fruits are what we call "deaf"; no signs of an embryo are to be found within. Thus, in this plant, no brood-body has been produced; it is impossible to say whether or no, at some former period, this plant ripened brood-bodies in its unfertilized ovules. Why the male plants of *Chara crinita* are absent from the Baltic, and those of *Gnaphalium alpinum* from the Arctic regions, are puzzles as yet unanswered. In *Chara crinita* it is only on the coast-regions that male plants are wanting; inland, male and female plants grow side by side. Possibly, climatic conditions and the vicissitudes to which our existing Flora has formerly been subject have brought this about, but we lack the data for continuing the discussion further.

If, in the plants enumerated, parthenogenesis be but a special case of offshoot formation, it is a matter of indifference which cells within the ovule are the starting-points for the brood-bodies. In *Catebogyne*, in addition to the egg-cell, other cells belonging to the wall of the embryo-sac are concerned in the production of brood-bodies. Cells quite outside the embryo-sac can also initiate these offshoots: in which case they project as little papillæ into the cavity of the embryo-sac, where they continue their development. In this way several embryos may arise side by side, a condition which has been termed *Polyembryony*. This phenomenon occasionally takes place in the ovules of hermaphrodite flowers, in which a normal pollination and passage of pollen-tubes to the micropyle occur. This is the case in certain *Liliaceæ*, polyembryony having been observed in species of

Funkia and *Allium*, in both of which normal fertilization takes place. It is interesting to note that in the case of *Allium odorum* recent investigations show that the accessory embryos arise actually from the *antipodal cells* (cf. pp. 416, 417), i.e. from cells at the base of the embryo-sac which, in ordinary cases, simply atrophy. Usually one embryo only arises from this source, but occasionally all three antipodal cells develop into embryos. The ultimate fate of the embryo arising (by fertilization) from the egg-cell and of those arising from the antipodal cells has not been ascertained.

A peculiarity of parthenogenesis consists in the fact that the brood-bodies arising in the ovules assume the form of embryos, not distinguishable from embryos resulting from fertilization of an egg-cell. Little tubers or buds produced in the ovary in places of ovules, as in *Amaryllis* and *Crinum* (cf. p. 44), partake of the nature of branches of the plant producing them; but the offshoots which arise within ovules are not branches but young plants, provided with root, stem, and leaves, and they are nourished by a special tissue which cannot be interpreted as a portion of the axis of the young plant. These offshoots arising within the ovule possess a new and independent axis, and herein exhibit an essential difference from the offshoots described in the last chapter. Why these offshoots in the ovules always assume the guise of embryos is a problem which we shall not solve, perhaps, until we have more knowledge as to the essential differences in property between the protoplasm of the ovule and that of other plant-organs.

HETEROMORPHISM AND ALTERNATION OF GENERATIONS.

A sight of the sea-anemones and ever-varying polyps and corals, viewed through the blue-green waters of a shallow bay, at first suggests a kaleidoscopic assemblage of blossoming plants. At a distance the crowns of expanded tentacles resemble red and purple Asters or the flowers of *Mesembryanthemums*; the skeletons of these organisms are not unlike, in their ramification, the branching of some tufted plant. The corals and polyps, like plants, are denied free movement, and like red and other seaweeds, are attached to their stony substratum. Very appropriate then, in view of their characteristic appearance, is the name of Zoophytes which Zoologists gave to these animals.

And in their internal structure and mode of life they present certain remarkable points of resemblance to plants. In many species the single individuals which are joined together into a colony behave quite like the organs of a body, or the members of a single organism which discharge different functions. There is a division of labour amongst the individuals or polyps of the colony. One branch of the colony is concerned in the acquiring of nutrition, another in reproduction, yet they have a common digestive cavity, so that the juices obtained by one portion may be shared by others which cannot take them up from the environment for themselves. To this differentiation amongst equivalent members we may apply the term *Hetero-*

morphism; it will be seen in the sequel that Heteromorphism is a condition of wide occurrence amongst plants.

Zoophytes propagate themselves in two ways. They may produce buds which grow into new individuals, just as buds arise on the branches of a tree and grow into new branches; and, like the latter, the products of these buds remain attached to the part of the colony producing them, so that ultimately the extent of the colony is considerably augmented. In many Zoophytes, especially in the Polypomedusæ, certain branches of the non-sexual polyp-form assume the form of cups or capsule-like structures in which buds arise which grow into disc-like, free-swimming medusæ, with a crown of tentacles. These medusæ contain sexual organs, and from each of their fertilized eggs an embryo arises which becomes attached to the sea-bottom, and grows either into a non-sexual polyp or into a group of sexual medusæ. In the last-named event the pear-shaped embryo, after swimming about for a while, becomes attached by its pointed end. On its body arise a number of ring-like furrows, which gradually deepen until the cone-shaped embryo is segmented into a number of transverse discs. Ultimately the cone disarticulates and the discs swim away as medusæ. These medusæ are sexual persons, and from the fertilized egg-cells, either sexual or non-sexual generations may arise. This alternation of sexual and non-sexual persons is known as *Alternation of Generations*.

Thus within the limits of the Zoophytes we see displayed two entirely distinct things. First, heteromorphism, which gives us equivalent polyps on the same colony, variously modified for the discharge of different functions; secondly, alternation of generations, in which medusa-forms (sexual persons) arise by a process of budding from polyp-forms (asexual persons), and give rise, by a sexual process, to fresh polyps. Alternation of generations is an alternation of sexual and asexual individuals, the one giving rise to the other.

Both these phenomena are widely manifested amongst plants. The plant-body amongst the Flowering Plants may be regarded as an assemblage of shoots. Each shoot or branch-system consists of a series of members, of which the upper and younger ones are developed with the assistance and co-operation of the lower and older. These shoots are all united together, and the tissue which unites them, with its conducting-tubes and air-lacunæ, may be regarded as an organ common to them all. From the fact that the several shoot-members have the capacity of independent existence, when separated from one another, they have been regarded as individuals and termed "Anaphytes" (*cf.* p. 6). Shoots, united together into a plant-body, possess a common household, and division of labour is manifest amongst them. The Anaphytes of the foliage region serve especially for the preparation of food-stuffs, those of the flowering region for the production of sexual cells and fruits. Shoots of the latter kind are termed flowers, of the former foliage-shoots. Shoots arise from buds, and these may be similarly distinguished into flower-buds and foliage-buds. Those which arise from foliage-buds remain, for the most part, attached to the plant-body, appearing as branches of the same; those, on the other hand, which arise from flower-buds ultimately disarticulate,

leaving a scar. Thus we see the shoots of a plant-body are variously modified, and we may speak of a *heteromorphism* in this connection analogous to that existing amongst the polyps of a coral.

It not infrequently happens, amongst purely foliage-shoots, that the lateral shoots (or anaphytes) bear foliage quite unlike that borne by the shoot that gives them origin. In many perennial shrubs and trees a long series of asexual shoots arises, of which the lowest and highest are so different, that one might easily suppose them to belong to different species of plants; or that a gardener had grafted a bud of another species upon the plant. The shoots of young Ivy plants (*Hedera Helix*), whether creeping on the soil of the forest-floor, or climbing up the trunks of trees or steep rock-faces, bear shortly-lobed, white-veined, dull-looking leaves, and produce a large number of attachment-roots which hold the shoot to the substratum. The shoots of an old plant, however, developed high up on the tree crown, or over the top of the wall, bear bright shining, heart-shaped leaves without conspicuous veins, nor do they produce roots at all. It is this latter class of shoots alone which bring forth flowers; the creeping shoots never do so (*cf.* vol. i. p. 709).

This contrast between the appearance of the shoots of a young plant and those produced in later years is much more marked in the Aspen (*Populus tremula*). The foliage-leaves of the first year's shoots are triangular, cordate at the base, and only shortly stalked, they are also hairy on the under surface; those arising on the shoots of a thirty-year-old Aspen are circular in outline, smooth on both sides, and provided with long petioles. Similar is the case of many Willows, Oaks, and Myrtaceæ; in the last-named family the Australian *Eucalyptus globulus* is worthy of mention. The leaves on its first year's shoot are sessile and cordate at the base, whilst on the grown tree they are stalked and curved like a boomerang. Very marked, again, are the differences in the character of the foliage-leaves on the successive shoots of the Junipers (e.g. *Juniperus excelsa*, *japonica*, *phœnicea*, *chinensis*, and *Sabina*). The leaves on the younger branches (for the first ten years about) are acicular, stiff and spreading; those on the shoots of later years are short, scale-like, and closely imbricating. Worthy of note in this connection is the contrast of long and short branches seen in many Conifers, e.g. the Larch (*Larix*). Though the actual leaves are not dissimilar, their insertion is, and the length of the shoots producing them. Whilst the short branches do not attain a greater length than 1 centimetre, the long branches reach to 15 or 25 cm.; to this contrast is due in large degree the altogether peculiar physiognomy of the Larch-tree, as shown in fig. 354 (*cf.* also, fig. 337¹, p. 443).

The fruit-trees in our orchards are some years covered with blossom, and, with a propitious summer, they are weighed down with fruit in the autumn. Such "bumper" years are generally followed by a series of lean years, in which little fruit is ripened, or flowers are hardly produced at all. The same thing is observed in forest trees. There is a saying that Firs and Larches only form their cones in plenty once in seven years. This is so far right in that a good

fruiting year is followed, in these trees, by several sparing ones; so much so that it suggests that the trees are exhausted by the heavy production and require time in which to recover, and, by the formation of non-flowering shoots with green foliage, to manufacture and lay by stores of food-material. So also in



Fig. 346.—Alternation of Generations in Ferns.

- ¹ A Fern-prothallium seen from the under side; archegonia are present amongst the rhizoids and towards the sinus at the top, antheridia on the margin below. ² Longitudinal section of an archegonium showing the egg-cell (shaded) in its ventral portion. The canal leading to the egg occupies the neck-portion. ³ Longitudinal section of an antheridium showing the spermatozooids coiled up within. ⁴ Antheridium discharging its spermatozooids. ⁵ Commencement of the asexual generation. The first simple frond of the young fern-plant (sporophyte) is held aloft, whilst a root descends into the ground. The young fern-plant is still attached to the prothallium. ⁶ Complete sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) with its fronds showing sori. ⁷ Under surface of a pinnule of the sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) showing the linear aggregations of sporangia (sori), with lateral indusia. ⁸ A young prothallium arising from a spore; the spore is below. ⁶ natural size; ¹ $\times 8$; ², ³, and ⁴ $\times 350$; ⁵ $\times 6$; ⁷ $\times 3$; ⁸ $\times 240$.

many low herbs. Now and then the Orchids in the meadows flower in immense profusion, and we say it is a good "Orchid year"; then follow years in which, in the same localities, hardly an orchid-flower is to be found.



Fig. 347.—Tree-ferns (*Alsophila*) in Ceylon (drawn from nature by Ransonné).

The impulse to the production of flowering-shoots cannot entirely depend on the prevailing climatic conditions of the year in which the flowering takes place. For in the autumn of the previous year the bud is already laid down, and one can tell by dissecting it whether it will form a flowering or a foliage-shoot. In associating climatic conditions with flower-production, it is the summer of the year previous to flowering which must be taken into account. This is well illustrated by the seasons of the years 1893 and 1894. The summer of 1893 was, as is well known, remarkable for its warmth and long-continued sunshine. This was followed in 1894 (to take an example to hand) by the flowering of many plants in Kew Gardens which are hardly ever known to flower there in the open,



Fig. 345.—*Rhipidopteris peltata* showing sterile fronds to the left, and fertile ones to the right.

under ordinary circumstances. Of these it will be sufficient to mention two Gymnosperms, *Ephedra* and the Maidenhair tree (*Ginkgo biloba*).

It is easy to observe the fact that in a big tree, of which one side is in the full sun whilst the other is shaded, the shady side produces foliage-shoots for the most part, whilst the sunny side blossoms freely. Nor can one resist the conclusion that it is the sunshine which stimulates the flowering. The same thing is shown by plants, which, growing in dense forest shade, remain without flowers from year to year: but as soon as the trees about them are felled, and the light gains entrance, form flower-buds, and ultimately blossoms and fruits. The advantages accruing to the plant by this change in its surroundings have already been indicated on pp. 394 and 459; but what immediate influence the sunlight has on the building capacity of the plant,

and how it is that the tissue which, in the shade forms a foliage-bud should in the sunshine form a flowering shoot, must for the present remain unanswered.

And now, as regards *Alternation of Generations*. The relations between the sexual and asexual generations are very various in different portions of the vegetable kingdom. In some groups of plants the two generations are obvious and distinct, in others it is very difficult to draw the line between them. In the Ferns, Horsetails, and Vascular Cryptogams generally, the two generations are quite distinct and easily recognizable. In the Ferns the generation which bears the sexual organs (=sexual generation or oophyte) takes the form of a small, expanded plate of cells, from the under side of which delicate hair-like rhizoids are developed which penetrate the soil (see fig. 189¹⁶, p. 11, and fig. 346¹). This plate-like structure is usually known as the *prothallium*; it is either heart-shaped or ribbon-like and lobed, attaining a length of from .5 to 1 centimetre. The sexual organs

are borne on the under surface of the prothallium; the antheridia as little hair-like structures distributed over the surface (fig. 346³), the archegonia, flask-like in form, and having the expanded ventral portion sunk in the substance of the prothallium and the neck projecting (see fig. 346²). In the majority of Ferns both sorts of sexual organ occur on the same prothallium, the archegonia on the central parts and in the region of the notch or sinus, the antheridia towards the margin and on the lobes. Fertilization is brought about by the escape of spirally twisted



Fig. 349. — *Platycerium alcicorne* (drawn from nature by Selleny).

spermatozoids from the antheridia (fig. 346⁴), which enter the neck of the archegonium, one of them fusing with the egg-cell contained in the ventral portion of that organ (fig. 346²). We may regard the fertilized archegonium as the fruit. It does not become detached from the prothallium, but the fertilized egg-cell develops *in situ* into the next (or asexual) generation, which differs altogether from the sexual one. The egg-cell divides into several cells, one of which gives rise to the young stem, another to the first frond, a third to the primary root, whilst a fourth forms a sucker or "foot", which maintains communication for some time with the tissues of the prothallium (*cf.* fig. 346⁵). Soon after the first simple frond is expanded, a second is formed, and the young fern-plant is now able to continue its development independent of the prothallium. The prothallium now dies away, and in its place

we have the young fern-plant with its fronds (*cf.* fig. 346⁶). The fern-plant bears no sexual organs, and must be regarded as the asexual generation (or sporophyte). Its first fronds provide the necessary food-materials for the production of new fronds, which arise in increasing numbers from the stem-apex; as a rule the stem remains short, or it may be elongated horizontally as a rhizome, or, in the Tree Ferns (*cf.* fig. 347), it develops into an erect caudex bearing a tuft of green fronds at its apex. In addition to their purely assimilating function, the fronds are concerned in the propagation of the plant, and produce quantities of spore-cases (or sporangia) containing spores. These sporangia arise in clusters, known as sori, and are usually situated on the under sides of the fronds (see figs. 346⁶ and 346⁷, and fig. 189, p. 11). In the majority of Ferns these two functions—assimilation and spore-production—are performed by one and the same frond, and there is no especial difference in structure between the assimilating and spore-producing portions. But in the so-called “Flowering Fern”, or Royal Fern (*Osmunda regalis*), these two portions of the frond stand out in marked contrast; the topmost pinnules of the frond are entirely covered with sporangia and light brown in colour, whilst the lower portions are bright green, and quite destitute of sporangia. In the Hard Fern (*Blechnum Spicant*) and Parsley Fern (*Allosorus crispus*) there is a distinction between the sterile and fertile fronds, the pinnules of fronds which bear sporangia being much narrower than those of purely assimilating fronds. In *Rhipidopteris peltata*, again, the fertile fronds are disc-like, whilst the assimilating fronds are branched and filamentous (see fig. 348); in *Platynerium aleicorne* the fertile fronds are branched like a reindeer horn, whilst the sterile ones form great green discs in close contact with the bark of the tree on which it grows, and remind one of huge prothallia (see fig. 349). As soon as the spores are mature they are discharged from the sporangia and scattered by the wind. Falling on moist earth, on the bark of a tree, or in a rocky cleft, they germinate, producing prothallia, upon which the sexual organs are borne (*cf.* fig. 346⁸). Thus in the Fern, two stages are well shown in the life-cycle, (1) the prothallium, the sexual generation or oophyte, and (2) the fern-plant, the asexual generation (or sporophyte), which bears spores, these in turn give rise to the first generation again.

In the Horsetails (*Equisetaceæ*), which have been figured and referred to at p. 14, a similar alternation of generations occurs. The fern itself is the asexual generation, and bears cones of sporangium-producing scales. From the contained spores prothallia are formed. In several species of Horsetail (e.g. *Equisetum sylvaticum*, fig. 190⁷, p. 14) one and the same shoot bears the organs of assimilation and spore-production; whilst in other species (e.g. *Equisetum arvense*) these functions are relegated to distinct shoots; *i.e.* shoots formed in spring, which terminate in cones (fig. 190², p. 14), and others formed later, which bear numerous green assimilating branches, but no cones (fig. 190¹, p. 14).

In the group of the Lycopodiinæ very interesting conditions prevail. In the so-called Club Mosses (*Lycopodiaceæ*) the plant is much branched, and in a great many species of *Lycopodium* (e.g. *Lycopodium annotinum*, fig. 378) the shoots end

in cones of closely-fitting scales, each of which bears a sporangium. The spores in *Lycopodium* are all alike, and on germination form prothallia, which bear antheridia and archegonia. It is interesting to note in passing that we have only become acquainted with these prothallia in recent years, and for the most part in exotic species. The prothallia of a limited number of European species, however, have been seen. Included in the Lycopodinae is the genus *Selaginella* (cf. fig. 111¹, vol. i. p. 421), resembling *Lycopodium* in its moss-like habit, but differing from it in that *two sorts of spores* are produced. These spores, known as *macrospores* and



Fig. 350.—Alternation of Generations in Mosses.

¹ A spore germinating. ² A moss-protonema. ³ Protonema giving rise to a bud from which will arise a leafy moss-shoot. ⁴ Longitudinal section of tip of a male shoot of a moss-plant; antheridia are present between the scales. ⁵ Tip of a female shoot with archegonia; two of them have much enlarged due to the swelling of the young sporogonium within. ⁶ Leafy female shoot of a moss-plant with fully developed sporogonium at its tip. Spores arise asexually in the terminal capsule. 1, 2, 3 $\times 350-400$; 4 $\times 15$; 5 $\times 80$; 6 $\times 5$.

microspores, arise in different sporangia in the same cone, in many cases. The macrospores are relatively large, and are contained four in a sporangium; the microspores are small, and a large number of them is present in a sporangium. The prothallia resulting from their germination are of two kinds: the macrospore gives rise to a female prothallium which bears archegonia; the microspore to a much reduced male prothallium bearing a single antheridium. The sexual generation—which in the Fern consists of *one structure*, the prothallium—here consists of *two structures*, the male and female prothallia. After fertilization the archegonium gives rise to a new, asexual *Selaginella* plant.

This differentiation amongst the spores in *Selaginella* (in consequence of which the plant is termed *heterosporous*, in contradistinction to Ferns, and *Lycopodium*,

which, having one sort of spore only, are termed *homosporous*) is of interest, since it leads on to the condition prevailing in Flowering Plants. In these the alternation of generations is not obvious, no recognizable and detached sexual generations being seen. But on certain shoots of flowering plants (*i.e.* in the flowers) sporangium-bearing leaves are borne; these are the stamens and carpels respectively. The sporangium borne by the stamen is the pollen-sac, and the contained pollen-grains are the microspores. The microspore or pollen-grain, when it germinates on the stigma (or in the micropyle, in Conifers, *cf.* p. 418) forms a pollen-tube, which contains the male fertilizing element, corresponding to a spermatozoid. Of course the conditions of fertilization in the Flowering Plant are altogether different from those obtaining in the Vascular Cryptogams, and motile swimming spermatozoids are no longer produced. The sporangium borne by the carpel, on the other hand, is the ovule, and the embryo-sac contained within the ovule is regarded as the macrospore. As a rule but one macrospore is met with, but in certain Amentaceæ (*e.g.* *Pinus*, see fig. 314A, p. 412) more embryo-sacs (macrospores) than one are present. In the Flowering Plant the macrospore is not shed from its sporangium (ovule), but germinates *in situ*, forming an egg-apparatus (*cf.* fig. 316 and p. 417), and certain other cells, which ultimately form the endosperm. These structures are regarded respectively as corresponding to the archegonium and female prothallium of such a heterosporous Vascular Cryptogam as *Salvinella*. If the contents of the embryo-sac in Gymnosperms (see p. 415) and in Angiosperms (see p. 417), respectively, are compared with the female prothallium of *Salvinella* or other heterosporous Vascular Cryptogam, it will be seen that the Gymnosperm shows the greater agreement. In it the archegonia are still quite recognizable as such, though these now take part in quite a different type of fertilization. In all Flowering Plants (Gymnosperms and Angiosperms) as opposed to the Vascular Cryptogams, the microspores produce pollen-tubes in the vicinity of the ovules, and these penetrate to the embryo-sac (macrospore) and fertilize the egg-cell. Consequently the counterpart of the archegonium is not exposed, as it is in Vascular Cryptogams, in which a free-swimming spermatozoid has to gain entrance.

Thus we see that in Flowering Plants the female prothallium or sexual generation is hidden away in the embryo-sac, and is never an independent structure. This fact is correlated with the different manner of fertilization which obtains in Flowering Plants as compared with Vascular Cryptogams.

In the Mosses the sexual organs are formed at the tips of little leafy shoots; fertilization is much as in Ferns, and from the fertilized egg a new (asexual) generation arises. This generation, known in Mosses as the sporogonium, consists of a stalk (the seta) terminating in a spore-capsule above. The sporogonium develops within the archegonium on the sexual generation of the Moss. The base of the seta penetrates some distance into the fertile Moss-shoot, and is in this way able to absorb nourishment. As the sporogonium elongates, the archegonial wall stretches with it up to a certain point, then it breaks across transversely and the upper portion is raised up on the capsule as a sort of hood or extinguisher (the

calyptra, see figs. 350⁵ and 350⁶). Ultimately this hood is thrown off and the capsule, within which quantities of spores are produced, opens. The spores are readily distributed by the wind shaking the capsule on its stalk. It should be noted that in Mosses this asexual generation (the sporogonium) never becomes independent of the sexual Moss-plant: the base of its stalk always remains embedded in the tissues of the sexual generation. In the Ferns, on the other hand, the



Fig. 351.—Alternation of Generations in Mosses. Various forms of sporogonium, which as the asexual generation have been produced at the tips of leafy shoots.

¹ *Splachnum luteum*. ² An unripe capsule of the same. ³ A ripe and open capsule of the same. ⁴ *Splachnum vasculosum*. ⁵ Longitudinal section of a ripe capsule of this Moss. ⁶ *Splachnum ampullaceum*. ⁷ An unripe capsule. ⁸ A ripe capsule of the same. ⁹ and ¹⁰ *Schistostega osmundacea*. ¹¹ A ripe capsule of the same. 1, 4, 6, 10 natural size; 2, 3 \times 2; 7, 8, 9 \times 10; 11 \times 15; 5 \times 100.

asexual generation (=the Fern-plant), though at first drawing nutriment from the prothallium (cf. p. 475) by its "foot", soon becomes quite independent, the prothallium dying away. The form of the sporogonium is very varied in different groups of Mosses. In fig. 351 are shown the sporogonia of a number of Mosses, including species of *Splachnum* (*S. luteum*, *S. vasculosum*, and *S. ampullaceum*), a rare form occurring on the excrements of cattle, reindeer, &c., that of the already-mentioned Luminous Moss (*Schistostega osmundacea*, cf. vol. i. p. 385); and in fig. 191, p. 16

those of *Polytrichum*, *Bryum*, *Hylocomium*, *Andreaea*, and *Sphagnum*. The spores of the asexual generation germinate on a moist substratum, giving rise to a tubular filament which becomes segmented, and gives rise to a considerable growth of simple character, known as the *protonema* (see fig. 350²). Certain rows of cells of the protonema are colourless and penetrate the ground as rhizoids, the others are extended on the soil and are bright green in colour. After a while bud-like



Fig. 352.—Asexual and sexual reproduction in Saprolegniaceae.

¹ Formation of asexual zoospores in *Achlya*. ² Oogonia with antheridia and fertilizing tubes. ³ Fruit. All figures $\times 300$. (After Sachs.)

structures arise here and there upon the protonema (see fig. 350³); these develop into leafy Moss-shoots, upon which the sexual organs are borne—usually in little clusters. Thus, in Mosses, the sexual generation has two stages; the protonema and the leafy Moss-plant. From the latter arises the asexual generation or sporogonium. In many of the Liverworts the sexual generation is much simpler, consisting of a thallus, in which the arche-gonia and antheridia are sunk. However, a great variety

is met with amongst them, but the main relations of the sexual and asexual generations are much as in Mosses.

It will be noted that in Mosses the sexual generation is much more complex a structure than the corresponding structure (the prothallium) in Ferns. The asexual generation, on the other hand, in Mosses is never independent, whilst in Ferns it becomes so quite soon and attains, in the latter group, to much greater structural complexity than in the Mosses.

Amongst the large assemblage of simple plants which together constitute the class Thallophyta we find in some forms an incipient alternation of generations on the lines already described for Mosses, Ferns, &c.; in others there is no suggestion of

such alternation; and in others again (such forms are numerous), an alternation occurs, but of a character quite different from that of higher plants.

First we will mention such as show an alternation of generations not unlike that of the Fern. It will be remembered that in the Fern there is a simple prothallium upon which the sexual organs arise, and from the fertilized egg-cell a new generation, of considerable dimensions, is developed which produces asexual spores, these in turn giving rise to prothallia. In the group of the Red Seaweeds or Florideæ (*cf.* pp. 61, 62, and figs. 204⁷ and 204⁹, p. 53), the seaweed plant is the sexual generation and bears the rudimentary fruits with trichogynes and the male spermatia. After fertilization, a considerable growth is initiated, which results in a mass of spores being abstricted, these spores being in many cases inclosed in a sort of capsule, which develops concurrently with the spores. This capsular structure with its spores we may interpret as a very simple asexual generation comparable to the sporogonium of a Moss or to a Fern-plant with its spores. Of course this asexual generation is very ill-marked in the Red Seaweed, and it is difficult to quite draw the line between it and the sexual generation of which it forms a continuation. It has this in common with Mosses and Ferns; that from a single process of fertilization a numerous progeny of spores is begotten—spores which on germinating give rise to sexual plants again.

The brown Wrack, *Fucus*, is an example of a Thallophyte in which alternation of generations is not known to take place. In this seaweed every generation is a sexual generation, and the fertilized egg-cells, so far as is known, give rise—not to spores—but to new sexual generations. Its life-history is described and figured on pp. 51, 52.

And now we come to a type of alternation of generations, prevalent amongst green Algae and some families of Fungi, which seems to be quite distinct from the rhythmic alternation which obtains in the Mosses, Ferns, &c. The oft-mentioned

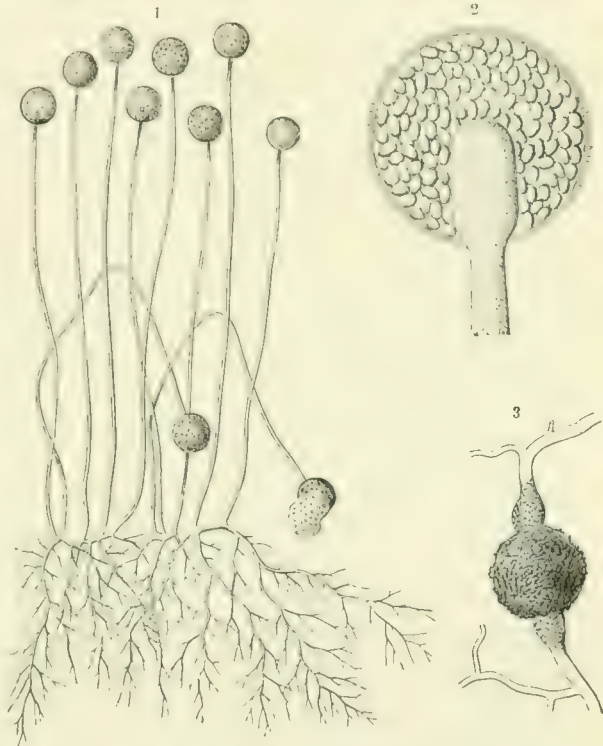


Fig. 353.—Asexual and sexual reproduction in the Mucorini.

1 Mycelium producing asexual spores in stalked sporangia. 2 A single sporangium in section. 3 Formation of a zygospore. 1 $\times 40$; 2 $\times 260$; 3 $\times 180$.

tubular Alga, *Vaucheria sessilis* (belonging to the family of the Siphonaceæ) will serve as an admirable example of what we mean. This plant reproduces sexually (cf. pp. 57, 58, and figs. 204⁵ and 204⁶, p. 53) by means of oogonia and antheridia of simple character; it also propagates itself by means of large asexual zoospores which it liberates from the tips of its tubular filaments (cf. vol. i. pp. 23, 24, and Plate I, figs. *a-d*). But these two classes of reproduction do not occur simultaneously upon one and the same plant; but rather, so it was till lately supposed, upon generations which alternated with one another either regularly or irregularly. Sometimes the *Vaucheria*-plant arising from a zoospore bore sexual organs, and from the fertilized egg-cell arose a non-sexual plant which gave rise to zoospores again; or a series of asexual generations followed one another, the series being terminated by a sexual generation, the fertilized egg-cells of which entered on a resting stage.

The meaning of this supposed alternation of generations in *Vaucheria* has recently been cleared up by Klebs in a series of very interesting culture-experiments. Without describing these in detail we may briefly indicate some of Klebs's results. If a number of young *Vaucheria*-plants be cultivated, three possibilities are open: the plants may produce sexual organs; they may be reproduced asexually by zoospores; or, finally, they may remain perfectly sterile. Klebs found that by appropriate treatment of plants, he could bring about any of these possibilities at will. Young plants placed in a 2-4 per cent sugar solution, and kept in the light at a temperature not falling below 3° C., invariably produced sexual organs in the course of some ten days. Other plants, which had been grown in a dilute nutrient solution of food-salts in the light for a short time, were removed to water and placed in the dark. These plants soon gave rise to enormous quantities of zoospores: in time these zoospores germinated, and the resulting plants in their turn produced fresh zoospores, and so on. The third condition, that of sterility, was obtained by keeping plants in strong sugar solution (10 per cent), and also by other methods. More than this, the same plants were caused to alter their mode of reproduction by varying the conditions; in this way it was possible to cause them at one time to produce zoospores and at another sexual organs. This brief summary is sufficient to show that a given *Vaucheria*-plant has no inherent tendency to reproduce asexually in preference to sexually, or conversely; and that its manner of reproduction (or its abstention from reproduction) depends on the conditions which prevail outside the plant. Thus, in *Vaucheria*, no true alternation of generations prevails in the sense in which it does in Mosses and Ferns, and every generation is potentially both a sexual and an asexual generation. It is the external conditions which call forth the one or the other.

In a great many other Thallophytes the same is no doubt true, though exact experiments have yet to be performed on the majority of them. We know it to be so in *Botrydium* and in the Water-net (*Hydrodictyon*) and in others. The Water-net (figured on p. 24) propagates asexually by the contents of its cells breaking up into very numerous (7000 20,000) swarm-spores (thallidia) which

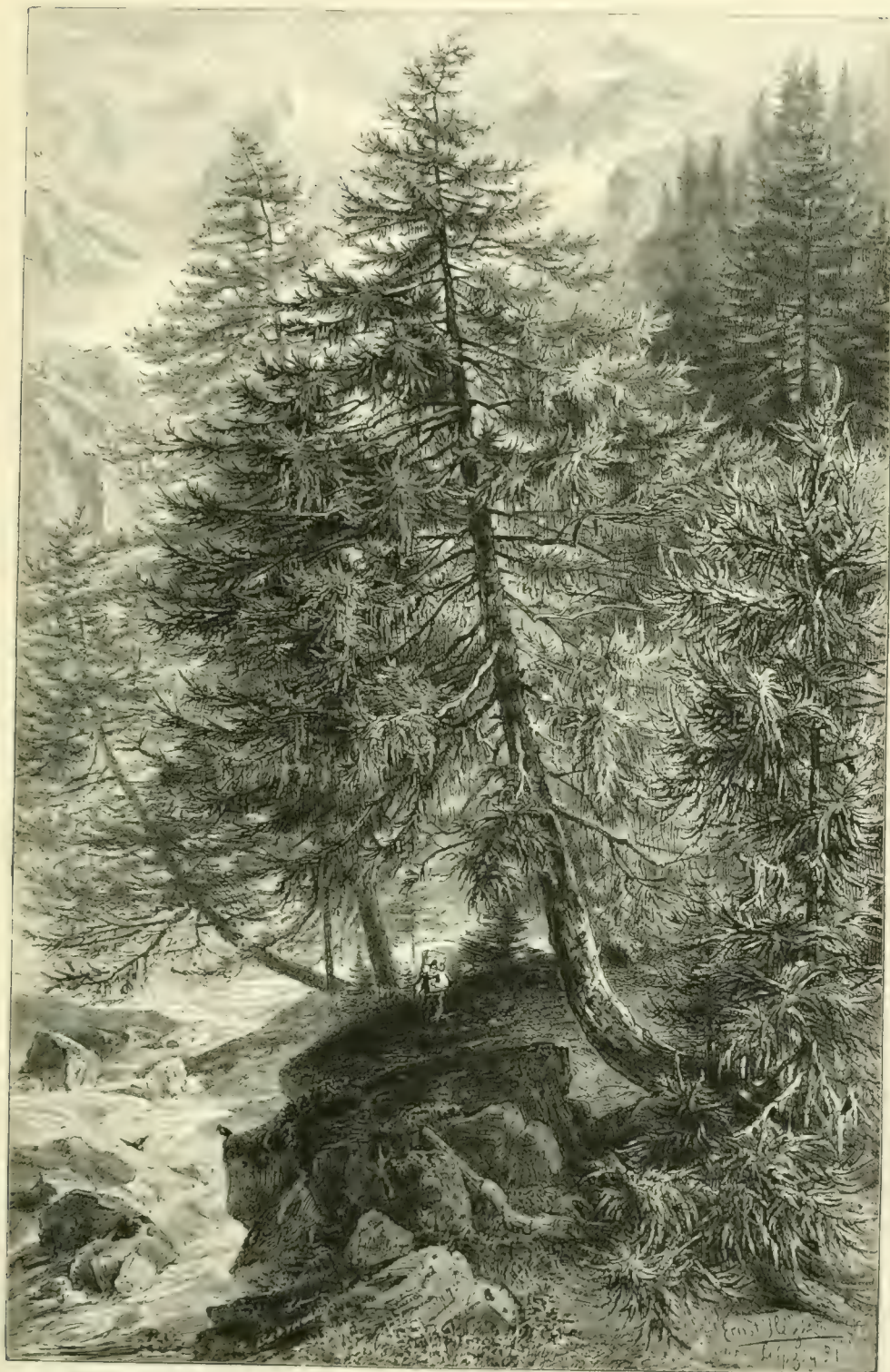


Fig. 354.—Larch-trees (*Larix europæa*).

do not forthwith escape, but swim about for a while within the wall of the cell in which they originate. Then they join together into a tiny net which escapes, ultimately growing to its full size (*cf.* vol. i. p. 36). In sexual reproduction a much larger number (30,000-100,000) of small motile bodies (gametes) escape and conjugate in pairs. Klebs has found here also that either of these methods can be produced at will by altering the conditions under which the plant grows.

Among the Fungi the Saprolegniaceæ show well-marked sexual and asexual methods of propagation. These are mould-like forms which attack fish and other aquatic animals upon which they are parasitic. Purely asexual reproduction occurs by means of zoospores which are liberated from long, club-shaped sporangia (fig. 352¹); whilst sexual reproduction (which may occur upon the same plant) takes place by spherical oogonia arising upon certain branches and antheridia as small lateral twigs below them (fig. 352²). The latter perforate the oogonium-wall with their "fertilizing tubes" (*cf.* the allied *Pythium*, p. 56), but curiously enough there is no real fertilization. Nothing has been observed to pass from the fertilizing-tubes to the egg-cells, and we must regard the process of fertilization here as obsolete. The egg-cells, though unfertilized, put on cell-walls (fig. 352³) and germinate, as one might say, parthenogenetically.

In the Moulds of the family Mucorini the mycelium establishes itself upon an organic substratum and produces, at one time, long-stalked sporangia (figs. 353¹ and 353²), and at another short sac-like outgrowths which arise in pairs near one another and conjugate, forming a zygospore (fig. 353³). Whether this or that method of reproduction prevails in these Fungi depends, most probably, on external conditions; indeed examples from amongst the Fungi could be adduced in which careful experiment has determined that this is the case.

In conclusion we may inquire how is it that alternation of generations is so widely distributed amongst plants, whilst in the animal kingdom it is of relatively rare occurrence. We obtain an answer to this question when we consider what are the distinguishing characters of those animals in which alternation of generations takes place. The corals, polyps, and other animals exhibiting alternation are in great part sessile organisms, attached to their substratum. But when a fixed organism propagates itself and distributes its kind, it must commit portions of itself to the winds or to currents of water, if new regions are to be occupied; a condition applying equally to plants and animals. Or, as an alternative, sexually-produced progeny may be liberated from the mother-organism and take up new positions. But sexual reproduction amongst fixed organisms requires rather special arrangements, and even with their aid is not invariably certain. Interference with fertilization may connote the extinction of the species; consequently a propagation by asexual means is of great importance for such organisms. By a definite alternation of the two methods, by a single act of fertilizing leading to an organism capable of multiplying itself almost indefinitely by asexual spores, a numerous progeny is ensured even from a single sexual union. Take the case of the Fern-

prothallium: from one fertilized archegonium arises a Fern-plant with many fronds and capable of producing millions of spores. Thus the species, whilst retaining to itself such advantages as may be inherent in the sexual process, is likewise able to diffuse itself in large numbers over an extended area by means of its numerous asexually-produced spores.

Allusion has been made to the advantages inherent in the sexual process. The investigation of their precise nature will be one of the main problems reserved for the second part of this volume. That a production of flowers and a ripening of seed is not *absolutely essential* for the maintenance and distribution of plants, seems not improbable—judging from the considerable number of plants which do well and flourish without them.

THE HISTORY OF SPECIES.

1. THE NATURE OF SPECIES.

Definition of Species—Specific Constitution of Protoplasm.

DEFINITION OF SPECIES.

The history of plant species is founded on the history of individual plants given in the first section of this volume, more particularly on the results afforded by investigation into the processes of reproduction and propagation. It deals with the description of the species from its origin to its end, and also takes cognizance of the replacing of extinct species by new ones. The execution of this task is less easy than the representation of the life-history of the individual which can be deduced from direct observation and experience. It being possible to follow the course of even long-lived individuals, beginning with the origin of the embryo and following it through all its life's stages, the meaning of certain vital processes as, for example, the pollination of the stigmas and the germination of the seeds can be understood. The origin of most of our present species, however, which have arisen without the aid of man, is shrouded in mystery; it occurred in long past ages and we are obliged to fall back on conjectures which, however intelligent and however they may be supported by carefully weighed considerations, are still only conjectures after all. For purposes of direct observation we have only the fossil remains of earlier times and the species which are living at the present day. By comparing these with one another, and by inferring the nature of extinct forms from that of living species, we are able to construct a chain of conclusions which after all may be regarded as the best available substitute for a history of species.

The most important foundations for these conclusions are afforded by the knowledge of the relations of living species to their environment, especially the recognition of those causes which bring about permanent changes of form, for this alone can elucidate the question of the origin of new species. Before discussing these important questions the nature of species must be described and we must understand exactly what is meant by a species.

The definition of a species was first introduced into science by Linnaeus, and the Latin word "species" owes its origin in this sense to the great master of Botany. Linnaeus laid down that each species consists of similar individuals which are related together by their origin, and which are the unaltered descendants of a common ancestor or pair of ancestors. It does not affect the value of the

definition that Linnaeus considered these ancestors to be creations of the "*infinitum ens*"; but it is very important that he recognized existing organisms as the continuation, the rejuvenated portions of one and the same living being, so that the species is not a figment of the human mind, but is something which actually has an objective existence.

Moreover, to decide which individuals are similar, *i.e.* of the same species, we take note of characters apparent to our senses, especially of the form and structure of the plant-body. Each species has its special features or characteristics, and all individuals possessing these specific marks are said to belong to the same species. Specific characteristics are hereditary, and are transmitted unaltered to the descendants. There are, however, some plant characteristics which are not inherited, but which may appear or not according as the individual develops in this or that place, and these must be regarded as the expression of certain external conditions which have an influence on plant-organization. They form the foundation for the existence of the variety, according to Linnaeus. The individuals of each species may vary, but the variations are not handed down to posterity; they change according to position and other external influences. Systematic Botanists since the time of Linnaeus have therefore to consider two kinds of distinguishing marks or characteristics: (1) those which are inconstant and not inherited; and (2) those which are constant under widely different external conditions and are hereditary. The latter determine the species, the former the variety. Each species may exhibit several varieties at one time, but its specific characteristics remain unaltered. If the specific marks should have undergone any alteration in the descendants, these will form a new species, or rather the appearance of an individual furnished with new specific marks forms the starting-point for a new species.

The relations of outward form and structure relied on by systematic Botanists in the identification of plant species depend of course on the plan of construction of the protoplasm of the species in question, and again only the specific constitution of the protoplasm determines this constructive plan. Before we can arrive at a correct idea of the nature of species, therefore, it is above all things necessary to obtain as clear a picture as possible of the relations of the protoplasm to the external visible form.

THE SPECIFIC CONSTITUTION OF PROTOPLASM.

Mention has previously been made of the remarkable fact that the species of a genus differing from one another in outward appearance also differ in respect of the scents secreted by them. Many Roses have different scents (*Rosa alpina*, *arvensis*, *cinnamomea*, *Gallica*, *Indica*, *Nasterana*, *pomifera*, *rubiginosa*, *sepium*, &c.), and a blind man could distinguish each species by the scent of its flowers. This is also true of species the foliage, stem, and roots of which emit odorous substances. By rubbing the foliage of different species of Thyme in one's fingers

(*Thymus Chamadrys*, *montanus*, *vulgaris*, *Zygis*, &c.), each will give off a peculiar scent; and when the roots or root-stocks of different Valerians (*Valeriana celtica*, *dioica*, *elongata*, *officinalis*, *Pha*, *saraticis*, &c.), or of different species of the Asarabacca genus (*Asarum Canadense*, *Europæum*, &c.) are dug up, though they all smell of valerianic acid or spikenard, each species has in addition a distinctive odour of its own. The edible Fungi (*Polyporus confluens*, *frondosus*, *ovinus*, &c.), Garlics (*Allium ascalonicum*, *Cepa*, *Porrum*, *sativum*, *Schœnoprassum*, &c.), various Currants (*Ribes alpinum*, *petraeum*, *rubrum*, &c.), and the Strawberries (*Fragaria collina*, *elatior*, *grandiflora*, *vesca*, &c.) all demonstrate most decisively that our olfactory nerves can distinguish between the different species of some genera. It might also be pointed out that it is no infrequent occurrence for one species of a genus to be poisonous to man while another is harmless, e.g. species of the Star-Anise genus (*Illicium anisatum* and *religiosum*), and of the fungal genus *Lactarius* (*Lactarius deliciosus* and *torminosus*). It is familiar to naturalists how precisely herbivorous animals can distinguish between different species of plants. The caterpillar of the Oleander Hawk-moth (*Sphinx Neri*) lives exclusively on the Oleander (*Nerium Oleander*), that of a small Mediterranean butterfly, *Thais Hypermnestra*, only on the Birthwort (*Aristolochia Clematidis*), that of the small Tortoise-shell Butterfly (*Vanessa Urtica*) only on the leaves of the large Stinging Nettle, and that of *Libythea Celtis* only on the foliage of the Nettle-tree (*Celtis australis*). Each caterpillar can at once distinguish the only species which suits it from numerous other similar ones. A friend of mine once found the caterpillar of a butterfly he did not know high up on the Gletscherstock in the Stubai, Tyrol, which he took into the valley with him intending to feed it until it became a chrysalis in order to obtain the butterfly. In the valley he placed it on about a hundred different plants in the hope that it would settle on one or other and use it as food. But it would not touch one of them, although caterpillars apparently suffer from voracious appetites. My friend now determined to revisit the spot where he had found the caterpillar and to set it at liberty there. When he did so it at once crawled as quickly as possible to a certain plant (*Cardamine alpina*) and attacked it with great eagerness. Later he discovered it to be the caterpillar of *Pieris Callidice*, which only feeds on the small Alpine Bitter-cress (*Cardamine alpina*). Generalizing from these instances, many more of which might be given, we are justified in assuming that the aromatic substances, alkaloids, acids, &c., which are manufactured in the plant metabolism are quite definite for each particular species. But it is equally obvious that a specific protoplasm is necessary for the manufacture of specific substances, or, in other words, that each plant-species with a certain definite form possesses also a definitely constituted protoplasm of its own.

The behaviour of different species with regard to temperature is especially worthy of note among the many observations which support this view. It is well known that seeds of various species which closely resemble one another in outward appearance differ greatly in the temperature they require for germination. Seeds

of one species are content with a low temperature, while those of another require much greater heat, although the eye can distinguish no difference in the structure of their coat, in their manner of storing reserve food, or in the structure of their embryos. The same may be said of the freezing of plants. Many Californian and Mexican Pines (*Pinus*) are very like those of Northern and Central Europe, and yet the one will be frozen to death as soon as the temperature sinks below freezing point, while the other can sustain winter temperatures of -20° C. without injury. There seems to be no reason why the South European Junipers, *Juniperus Oxycedrus* and *phœnicea*, which are apparently of the same structure as the similar species *Juniperus nana* and *Sabina*, should not flourish equally well on our mountain heights in the Central Alps, where the latter cover whole mountain peaks and send their roots into ground which is covered with snow eight months every year, and is frozen hard for months together. The common Ivy (*Hedera Helix*) grows in Central Europe without any protection from the fairly severe cold of winter; the S. European Ivy, *Hedera poetarum*, which is very similar to the common species, but can be distinguished from it by several external characteristics, requires a protecting roof in the gardens of Central Europe if it is to survive the winter unkilld by the frost. The same is true of two closely allied species of Marigold, viz. *Calendula arvensis* and *fulgida*, the former growing in Central, the latter in Southern Europe. In 1874 I sowed seeds of *Calendula arvensis* from the Rhine district side by side in the same garden-bed with seeds of *Calendula fulgida*, which had been gathered in Sicily. Very luxuriant plants which flowered in profusion grew up from both kinds of seeds. The first-frost in that year in the place where the experiment was made occurred on October 25th. *Calendula arvensis* was not injured: its foliage was fresh and green, and remained in this condition during the following days, although, until November 2nd, the temperature fell every night from -1.5° to -2.5° C., and in the morning the stem, leaves, and flowers were studded with hoar-frost. *Calendula fulgida*, on the other hand, was destroyed by the frost on the night of the 24th-25th October. Its leaves and stems withered and turned brown, and exhibited all the symptoms observable in death by freezing. In 1864 I found a *Cytisus* on the rocky shores of the Adriatic Sea at Rovigno, which closely resembled the wide-spread *Cytisus nigricans* of Central Europe, but which had certain distinguishing features. I named it *Cytisus australis*. Some of its seeds were collected, and from them strong young seedlings were obtained in the following year. These were planted in the Botanic Garden at Innsbruck with some seedlings of *Cytisus nigricans* of the same age from the Danube valley, near Mautern, in Lower Austria. Both grew under identical external conditions, and appeared to be equally vigorous. But during the winter the plants of the *Cytisus* from the shores of the Adriatic were killed by the frost, while those of the *Cytisus* from the Danube valley remained healthy and strong. The experiment was repeated with the two plants in the following year. Young plants were again raised from seed, but this time those from the Adriatic coast were protected against the cold, and in this manner they survived the winter without harm. Two years later both

the species of *Cytisus* developed flowers and fruits almost simultaneously under the same external conditions, and it was noticed that the same real, if insignificant, deviations were present in the external characteristics which had been present in the parents. This different behaviour of plants which, on account of their form, are described by the Botanist as distinct species, although closely allied, can indeed only be explained by assuming that the protoplasm, though having on the whole a similar constitution, is somewhat different in each species.

As a further confirmation of the assumption that the protoplasm of each species possesses properties which are lacking in that of others, we may take the case of the behaviour of pollen-cells in fertilization. If two kinds of pollen-cells are brought to the stigmas of a plant, *i.e.* pollen-cells of two different species, it usually happens that the one will fertilize the ovules with its pollen-tubes, while the other will be without effect. And yet the conditions are the same in both cases, and the difference in behaviour must therefore depend upon some difference in the protoplasm of the pollen-cells. Protoplasts which swim about as swarm-spores in the same drop of water, exposed to exactly the same condition of light, heat, pressure, &c., display a different behaviour if they belong to a different species. Those of one species will always twist to the right, those of another always to the left, some seek the light, others shun it for the darkest places. But since the protoplasm behaves differently under the influence of the same ray of light, the same temperature, and the same pressure, the cause must be sought for in the tiny mass of protoplasm of which each swarm-spore is composed.

The little amœbæ which proceed from the spores of Myxomycetes are protoplasts without a cell-wall; they live on dead parts of plants, where they feed, grow, divide, and multiply. When the right time comes these amœbæ fuse together to form a body known as a plasmodium, which is ultimately converted into a mass of sporangia (*cf.* vol. i. p. 572). Although the little amœbæ of different species cannot be distinguished from one another, and the plasmodia look like masses of formless protoplasm which only differ sometimes in colour, the resultant sporangial forms exhibit a remarkable variety of forms. From the plasmodium of *Stemonitis fusca* there arises a network of dark brown threads which is penetrated by and borne on a central axis like the shaft of a feather (see figs. 355¹ and 355²); from that of *Spumaria alba* is formed a white slimy mass resembling the "cuckoo-spit" of the Cicadellidæ and enveloping stem and leaves just in the same way (see fig. 355³); from the plasmodium of *Dictydium cernuum* there arises a globe-like lattice-work, with strong longitudinal ribs and delicate cross-bars, which is carried on a hooked stalk (see figs. 355⁴ and 355⁵); from the formless plasmodium of *Craterium minutum* arise stalked cups of a gray colour (see figs. 355⁶ and 355⁷); from that of *Acregria punicea* short stalked conical bodies not unlike Strawberries (see figs. 355^{8, 9, 10}); the plasmodium of *Lycogala epidendrum*, which penetrates the wood of dead tree-trunks, forms balls of the colour of red-lead, about a centimetre in diameter (see fig. 355¹¹), and out of the plasmodium of *Leocarpus fragilis*, which spreads over dead branches and twigs, proceed stalked egg-shaped sporangia, with

little brown coats (see fig. 355¹²). And all these peculiar forms arise under similar external conditions from apparently similar slimy and formless masses of protoplasm.

The same thing occurs in the Mushroom and Toadstool Fungi (Hymenomycetes) which develop in the mould of the forest ground and on the dead bark of tree-trunks. The mycelium is a network of white threads and strands, and neither the form of the colourless elongated cells composing the network nor

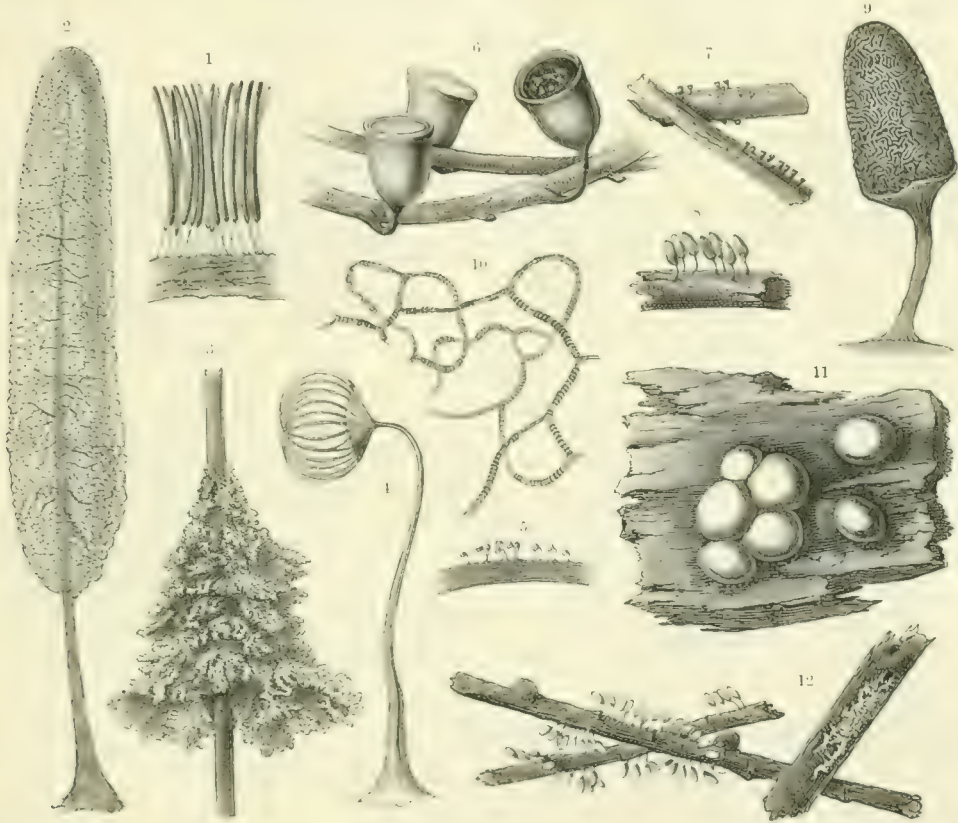


Fig. 355.—Myxomycetes.

¹ A group of sporangia of *Stemonitis fusca*. ² A single sporangium; $\times 6$. ³ Dendritic mass of sporangia of *Spumaria alba* on a Grass leaf. ⁴ Sporangium of *Dictydium cernuum*; $\times 25$. ⁵ A group of sporangia of the same. ⁶ and ⁷ Sporangia of *Craterium minutum*; $\times 25$. ⁸ Sporangia of *Arcyria punicea*. ⁹ A single sporangium; $\times 10$. ¹⁰ Part of the net-like capillitium of the same; $\times 160$. ¹¹ Fructification of *Lycogala epidendrum* on a piece of wood. ¹² *Leocarpus fragilis*; a plasmodium on the right; several sporangia on the left.

the protoplasm within the cells afford any indication by which we can judge the species to which the mycelium belongs. But how different are the fructifications proceeding from these apparently identical mycelia. In a part of the forest ground not twenty paces across there grow large specimens of *Boletus edulis* with chestnut-brown hemispherical caps; a little distance off a group of Chantarelles (*Cantharellus cibarius*), with yellow colour like yolk of egg, close by the Fly-agaric (*Agaricus muscarius* or *Amanita muscaria*), with snow-white stipe and crimson cap (*pileus*) spotted with white, and near at hand, from

a mycelium which has penetrated the bark and wood of a Beech-tree, grows the horse-shoe-shaped ashen-gray *Polyporus fomentarius* (cf. the accompanying Plate XIV., showing these Fungi amid their natural surroundings).

The fruits resulting from the conjugation of the unicellular Desmids are minute balls of protoplasm, and although they may originate from very different species, outwardly there is not the slightest distinction between them. But as soon as these small balls of protoplasm begin to develop, the greatest variety of cell-forms is the result. Each is fashioned after the form of the parent individuals which produced the fruit by conjugating. One cell will be half-

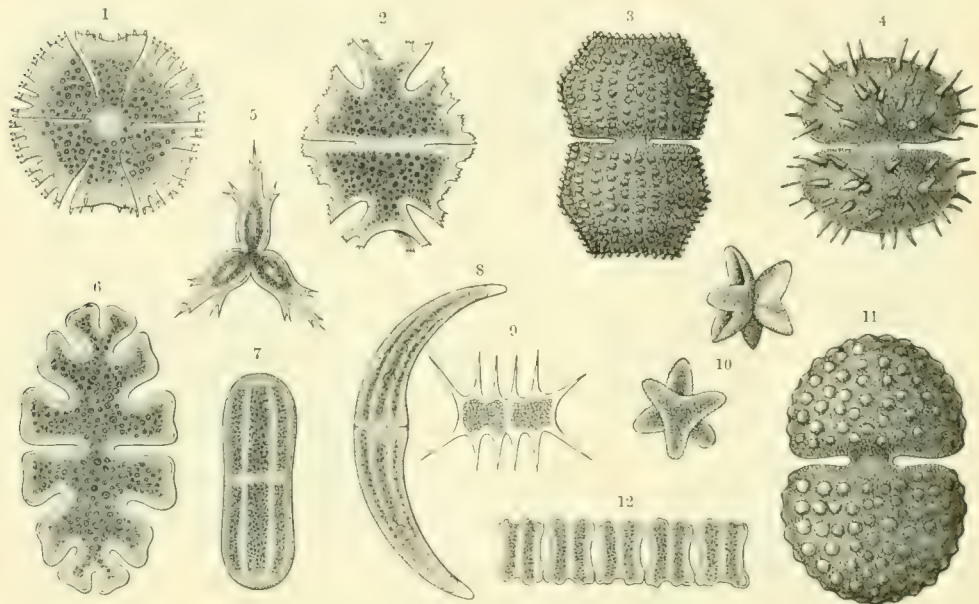


Fig. 356.—Desmidiæ.

¹ *Micrasterias papillifera*. ² *Micrasterias morsa*. ³ *Cosmarium polygonum*. ⁴ *Xanthidium aculeatum*. ⁵ *Staurastrum furcatum*. ⁶ *Euastrum oblongum*. ⁷ *Penium Brebissonii*. ⁸ *Closterium Lunula*. ⁹ *Xanthidium octocorne*. ¹⁰ *Staurastrum alternans* (two views). ¹¹ *Cosmarium tetraophthalmum*. ¹² *Aptogonium Desmidium*. All the figures magnified about 200 times.

moon-shaped, another cylindrical, a third angular and table-shaped, others again stellate and with manifold projections; some have a smooth surface, while the cell-wall of others is beset with spines or studded as if with pearls. The figures above, representing twelve different species of these Desmids, will give some idea of the multiplicity of their forms. And all these varieties spring from apparently identical masses of protoplasm, and develop side by side in the same drop of water, under the same illumination, the same temperature, and, generally speaking, under exactly the same external conditions and stimuli.

All these observations and results seem to indicate that the hypothesis as to a specific constitution of the protoplasm in each species is almost a necessary assumption. The word "constitution" has been purposely used instead of "composition", which might be taken to mean essentially the same thing were we



FIGURE 27. 1871

dealing merely with a chemical compound. Nothing would be more natural than a comparison with inanimate things whose outwardly perceptible features are the expression of a definite chemical composition, *i.e.* of a certain grouping of molecules and atoms which can be represented by a certain formula. But although this comparison is allowable in general, yet there is an essential difference between mineral and plant species. No formula can be given for the protoplasm of a species of plant, and the structure of a protoplast cannot be compared with that of a crystal. Each protoplast represents an organism which contains very many chemical compounds. It is able to renew them when required, and to modify their grouping as dictated by external stimuli. With these displacements there must of course be a temporary alteration of structure, *i.e.* of the grouping in the formed part of the protoplasm. But all these displacements and alterations take place in each species according to the same plan. The same chemical compounds, the same aromatic bodies, the same acids and the same alkaloids, &c., can alone be demonstrated. The recently-formed parts agree with those already present, and merely fill up the places previously assigned to them. This unalterable law of form which governs the working of the protoplasm in each species is, therefore, dependent on some structure of the protoplasm which is beyond the perception of our senses, and it is this which is termed the *specific constitution of the protoplasm*.

In the above-mentioned Desmids, which afford such especially instructive examples, and in numerous other unicellular plants where all the formative processes are carried on within a single protoplast, it is easy to see the connection between the outward appearance and the specific constitution of the protoplasm. It is more difficult in species where there is greater division of labour, a division into manifold cell-forms and a gradual succession of different members. One might compare the processes occurring in them with similar processes in mineral species, which, with the same chemical composition present a great difference in their outward form and appearance. Carbonate of lime, which forms the mineral species *calcite*, appears in four kinds of crystal-forms, but they all belong to the same system, and can be derived from one another. In the same way the varied cell-forms and tissues, as well as the cotyledons, foliage, and floral-leaves, which arise from the same plant in regular succession, are to be regarded as members of the same system, succeeding one another in definite rule, although the specific constitution of the protoplasm in the particular species undergoes no change.

At one time the idea was prevalent that there are two kinds of protoplasm, *idioplasm* and *cytoplasm*. To the former was assigned the formative activity, while the latter was regarded as merely a nutritive plasm or medium. Subsequently it was shown that in every protoplast there is a more definite part, termed the *nucleus*, which dominates the whole, especially in the building and renewal of the cell-wall, while it also takes a leading part in cell-division and multiplication. Thus the assumption that all formative processes are carried on through

the cell-nucleus was held to be correct. The fact of the constancy of species from generation to generation was therefore referred, especially, to the specific constitution of the cell-nucleus. Since the nucleus plays such an important part in the process of fertilization, which precedes the inception of the new individual in sexual reproduction, the hypothesis was put forward that the constancy of form in the offspring, or, in other words, the transmission of form, depends upon the specific constitution of the nuclei taking part in this process. Nor would this hypothesis be open to objection had not recent investigations shown it to be extremely probable that portions of the male cell other than the nucleus assist at this process. If, as it appears, more than the mere nucleus passes over from the pollen-tube at fertilization (*cf.* p. 417), how can we certainly allege that (to take a definite case) all the properties which the young plant inherits from its male parent are transmitted through the medium of the nucleus? If it be true that a certain portion of the cell-protoplasm takes part in this act, it must be proved that it plays only a subordinate part in the process (*e.g.* a nutritive function) before we can attribute to the nucleus the part of sole carrier of transmitted properties.

To the proposition that new individuals with the unaltered properties and characteristics of the species can only spring from the protoplasm of this nucleus, we cannot assent. Thousands of plant-species reproduce asexually in unaltered form by spores and other offshoots. As already stated so often, every young cell of a plant may be the starting-point of an offshoot or brood-body, and so may lead to the beginning of a new individual; and an individual produced in this way bears all the characteristics of the parent plant which produced the offshoot. It might even be asserted that the features of the species are more certainly inherited in the case of reproduction by offshoots and brood-bodies than in sexual reproduction, and in a subsequent chapter it will be shown that it is sexual reproduction alone which affords the possibility of posterity with altered characteristics.

The view that the part surrounding the nucleus of a protoplast, the cell-protoplasm or *cytoplasm*, has no formative importance is not borne out by the evidence of investigations into the origin of the so-called galls, which we shall discuss in detail later, nor by our knowledge of hybrids. On the contrary, hybridization causes not only an alteration of form in the new individual arising from the germ-nucleus, but also an alteration in the form of the tissue in the region of the ovule exclusively influenced by the cytoplasm, so that the effect of hybridization can be recognized even in the fruit which arises from the ovary. Every influence on the cell-nucleus must be transmitted through the cytoplasm. But it would be much more difficult to imagine that the cytoplasm remains quite indifferent to this transference than that it also experiences a change identical with or similar to that undergone by the cell-nucleus. Fortified by these considerations, we may then assume (1) that all protoplasts which we know are able to form the starting-points of new individuals have the capacity of transmitting the external form of the species unaltered to the offspring, and (2) not only a part

but the whole of the protoplasm of any species possesses the specific constitution of that species.

It is of the greatest importance not only for the existence of the species, but also for the origin of new species, that the protoplasm, by reason of its specific constitution, should always take the same form. New species can only arise from those already in existence. This is equivalent to saying that the protoplasm of an existing species must undergo alterations in its constitution. Living protoplasm with new specific constitution must be produced from what already exists. How such a fundamental alteration is effected can only be guessed at by roundabout methods. One has to be content, as in so many other instances, with the results of experiment and experience, and with ascertaining, above everything, what influences are capable of altering the outward form of a whole or part of a plant either temporarily or permanently.

2.—ALTERATION IN THE FORM OF SPECIES.

Dependence of Plant Form on Soil and Climate.—Influence of Mutilation on the Form of Plants.—Alteration of Form by Parasitic Fungi.—Alteration of Form under the Influence of Gall-producing Insects.—Origin of New Forms by Crossing.

DEPENDENCE OF PLANT FORM ON SOIL AND CLIMATE.

The little town of Kitzbühel, in the North-east Tyrol, has a very remarkable position. On the north rises the Wilde or Vordere Kaiser, a limestone chain of mountains with steep, pale, furrowed sides, and on the south the Rettenstein group, a chain of dark slate mountains whose slopes are clothed far up with a green covering. The contrast presented by the landscape in its main features is also to be seen in the vegetation of these two mountain chains. On the limestone may be seen patches of turf composed of low stiff Sedges, Saxifrages whose formal rosettes and cushions overgrow the ledges and steps of the rugged limestone, the yellow-flowered *Auricula*, the Rock-rose-flowered *Rhododendron*, and white-flowered *Cinquefoil* adorning the gullies, dark groups of Mountain Pines bordered with bushes of Alpine Rose; and opposed to these, on the slate mountains, are carpets of thick turf composed of the Mat-grass sprinkled with Bell-flowers, *Arnica montana* and other Composites, groups of Alpine Alder and bushes of the rust-coloured Alpine Rose—these are contrasts in the plant-covering which would strike even a cursory observer, and would lead a naturalist to ask what could have been the cause. No wonder that the enthusiastic Botanist, Franz Unger, was fascinated by this remarkable phenomenon in the vegetable world. In his thirtieth year, furnished with a comprehensive scientific training, he came as a doctor to Kitzbühel, and with youthful ardour he used every hour of leisure from his professional duties in the investigation

of the geological, climatic, and botanical conditions of his new locality, devoting his fullest attention to the relations between the plants and the rocks forming their substratum. The result of this study was his work, published in 1836, *On the Influence of Soil on the Distribution of Plants as shown in the Vegetation of the North-east Tyrol*, which marked an epoch in questions of this sort. The terminology introduced in the book found rapid entrance into the Botanical works of the time. Unger divided the plants of the district according to their occurrence on one or other of the substratums—in which lime and silica respectively predominated—into (1) those which grow and flourish on limestone only; (2) those which prefer limestone, but which will grow on other soils; (3) those which grow and flourish on silica only; and (4) those which, whilst preferring silica, will grow on other soils. He tabulated his results in such a way as to show clearly how certain species grew on the limestone and others on the silica-containing rock. Naturally these facts elicited a number of speculations. If the species *Gentiana Clusii*, *Hutchinsia alpina*, and *Juncus monanthos* growing on the limestone soil are replaced on the slaty soil by the similar (but yet distinct) species, *Gentiana acaulis* (*excisa*), *Hutchinsia brevicaulis*, and *Juncus tripidus*, we are justified in assuming that the difference in form is due to the influence of the substratum, *i.e.* to the influence of the chief materials in the rock—limestone and silica. But it has yet to be ascertained and proved, if possible by experiment, how this influence works; whether limestone and silica, respectively, introduce certain compounds into a plant, thus altering its outward appearance, or whether the difference is due rather to the fact that each plant-species requires so much lime or so much silica, and that when this is lacking in the soil the outward form becomes changed; or again, whether, after all, the physical properties of the substratum, its porosity, capacity for retaining water, and its specific heat, have not more influence on the form of plants than its chemical constitution.

Unger and his followers, amongst whom I enroll myself, thought they would obtain an answer to these questions by comparing the chemical composition of the plant-ash with that of the soil in which the plants were grown. But the results of careful investigations were anything but satisfactory. Both the substances named, the presence of which was supposed to be of special importance, could be demonstrated in most of the soils examined. Labrador felspar, hornblende, and other minerals in crystalline slate yield as much lime in the upper soil as is required by plants demanding or preferring limestone (classes 1 and 2, above), whilst the Limestones, which almost all contain clay, have silica enough for the needs of plants which demand or prefer silica (classes 3 and 4, above). Moreover, it was shown that plants have the power of obtaining materials which are valuable to them even when these occur around their roots in hardly appreciable quantity, so that they actually become accumulators of certain materials, and in this way a substance of which there are only minute traces in the underlying rock may be relatively abundant in the superficial layers of soil impregnated with the dead plant-remains (*cf.* vol. i. pp. 70 and 259).

Under these circumstances it is a matter of indifference whether 10 per cent or only traces of lime or silica can be demonstrated in the soil, and the hypothesis that plant-species which grow on limestone fail to grow on slate because they are not able to supply their need of calcium, or that the plants growing on slate cannot flourish on limestone mountains because they cannot obtain the necessary amount of silica, must be abandoned, as well as the assumption that these substances when absorbed as food serve as a stimulus to change of form.

I strongly supported this latter hypothesis at the time, and thought I should be able to strengthen and confirm it by careful cultural experiments. Seeds of several species which demand lime were sown in soil containing hardly perceptible quantities of lime, and the seedlings were watered with water devoid of calcium; in another place seeds of species demanding a silica-containing substratum were placed in soil which contained much limestone, and the seedlings were watered with lime-water. At first it seemed as if an alteration of form had actually taken place in some individuals. But this was a mistake, or rather, the alteration only consisted in the greater or less luxuriance of the foliage, lengthening or shortening of the stem, abundant or scanty development of flowers and the like. But no actual change of form which would be retained by their descendants could be obtained. The species of plants accustomed to lime, grown on a soil devoid of lime, presented a miserable appearance, with scanty flowers which ripened only a few seeds, whilst the silica-demanding species grown on lime-containing soil soon withered and died without flowering at all. The change of form, indeed the actual interchange I had anticipated between the closely allied species which grow on the two rocky substrata in a state of nature, did not occur at all.

If we still take the case of siliceous and calcareous plants, and regard the soil as the source of free inorganic substances which influence the plants, we are forced to assume that greater quantities of one substance will be injurious to one or other of them. The absorbent cells have the capacity of choosing between the substances at their disposal, but this capacity has a definite limit in every species. The cells can absorb as much as they require from a very weak solution of common salt, soda, gypsum, calcium bicarbonate, &c., but a concentrated solution of these salts may injure and destroy their structure and function. If it is allowed to act for any length of time on the cells whose function is to absorb inorganic nutriment, the death of the whole plant will inevitably result. If the Moss which grows on blocks of granite is watered with a saturated solution of gypsum; if the soil into which our Meadow-grasses send their roots is watered with a saturated solution of common salt; or if the humus in which the plants of an upland moor grow is mixed with sodium carbonate or calcium bicarbonate, the plants invariably perish, and the same mineral substances, which in a very weak solution are needful, or at any rate harmless, become poisonous when the solutions are concentrated. The fact that one species of plant prefers this and another that mineral substance (see vol. i. p. 73), however, renders it probable that the injurious effect of materials in large quantity in the soil varies, that a large quantity of

common salt would be injurious to one species, and an abundance of sodium or potassium salts to another. From the present standpoint of our knowledge concerning the absorption of inorganic materials by plants, therefore, Unger's classification, especially the expressions silica-demanding and silica-preferring, is no longer suitable, and it would be more to the purpose to speak of plants which are injured by lime, potash, &c.

The difference in the vegetation on the closely adjoining limestone and slate mountains met with in so many places in the Alps, and so well seen in the neighbourhood of Kitzbühel, where the climatic influences on the two ranges are identical, can be accounted for most satisfactorily in the following way. Plant-species which demand or prefer a siliceous soil are absent from limestone mountains wherever their roots would be exposed to more free lime than is beneficial; if present they would be weakened, and thus vanquished in the struggle with their fellows, to whom the larger quantity of lime is harmless, and they would eventually perish. These plants flourish luxuriantly, however, on slate mountains, because there the soil does not contain an injurious amount of lime. The absence of species, demanding or preferring lime, from slate mountains can be explained in the same way. When seeds are brought thither by the wind from the neighbouring limestone mountains and germination commences, their further development is visibly retarded; they dwindle wherever there is not much lime, and are overgrown and suppressed by the siliceous species which flourish there so luxuriantly. The brown or black mass formed by the decomposition of dead plant residues, known as humus, plays a very important part in the contrasting vegetation on limestone and slate mountains. To obtain a true idea of its significance it must first be pointed out that three distinct stages can be distinguished in the development of a continuous and intricate plant-covering. To the first stage belong the plants which settle down on the bare earth content with a substratum wholly devoid of humus; in the course of time they conquer the most barren rock, the barest boulders, and the dreariest shifting sands. The species of this group belong chiefly to the Lichens, Mosses, Grasses, Pinks, Crucifers, House-leeks, Saxifrages, and Composites, whose spores, seeds, and fruits are exceptionally well adapted for wind distribution, and can be transferred with ease to the steepest slopes and the most uncompromising crags. The second stage includes plants which require a moderate amount of soil mixed with humus; they establish themselves on the ground prepared by the first settlers, wresting it from them and taking possession, and then suppressing and overgrowing them entirely. These plants belong to very different families, whose distribution and establishment are effected in very many ways to be described subsequently. The third stage of development consists of plants for which the abundant humus stored up successively by the plants of the second stage is absolutely indispensable. Bog-moss, Lycopodiums, Sedges, and Heaths form the chief part of this stage. In the course of years the amount of inorganic materials in the soil which supports the plants of the third stage continuously diminishes. Plants which require a large quantity of inorganic salts languish, and are, moreover,

overcome by saprophytes which find a suitable habitat there and flourish in abundance. The decayed portions of Saprophytes contain relatively little inorganic material. No trace of lime (in particular) is to be found in their ash. In this way a superficial layer of humus is formed which actually excludes a large number of plants. The next deeper layer may contain a considerable quantity of inorganic salts, but they are valueless to plants rooted in the upper (humus) layer, as they cannot penetrate it. It has been shown by experiment that pure humus possesses the power of holding back materials which are soluble in water. It possesses this property to such an extent that if salt solutions are filtered through a layer of humus the water which escapes below is almost pure. It is therefore impossible for inorganic substances from the deeper layers of the soil, much less from the underlying rock, to reach the surface layer of humus in solution by diffusion; and if some mineral ingredients are not introduced by irrigation or flooding, the upper layer of soil consists of pure humus on which only saprophytic plants can flourish.

The formation of such layers of humus occurs much more easily and quickly on slate mountains than on limestone, because in the former the rock and the products of its decomposition retain water much better, and a uniform saturation promotes the development of humus, and also because on slaty soil the second stage of the development of the plant-covering consists of plants which require very few inorganic food-substances, and accordingly very few inorganic materials are yielded by the humus, which originates at the cost of the decaying portions of these plants. But a thick stratum of pure humus may also arise in course of time on limestone mountains. Only the soil must be uniformly moist in that spot, and neither sand nor mud must be deposited on it. If these conditions are fulfilled a deep humus will gradually spread itself over limestone rocks and debris in the third stage of development, the superficial layer of which will contain no trace of lime, but will afford an excellent soil for silica-loving plants (*i.e.* for those to which lime is injurious). The isolated occurrence of so-called siliceous or slate-plants on limestone mountains, even in the middle of a patch of plants which are characteristic of a limestone soil, may be naturally explained in this fashion.

The water which moistens the rock and soaks the soil has, apart from its mechanical action, the important function of opening up mineral substances and of forming solutions from which the absorbent plant-cells may take their choice. The atmospheric water which penetrates into the earth from above is especially valuable as a solvent on account of the carbonic acid gas it contains. It is immeasurably more valuable to every part of the soil which is riddled by the roots of living plants than the soil-water, so poor in carbonic acid, which collects on impervious strata of the soil and soaks upwards through the superficial layers.

The power of the soil to retain water depends mainly on the extent of breaking up undergone by the rock whose disintegration has formed the soil and upon the amount of clay which has arisen from this disintegration. But the amount of humus which in course of time has mixed with the disintegration and the decomposition products of the underlying rock is also an important factor, and thus very

complex conditions arise which render the estimation of the soil's capacity for retaining water very difficult. If permeable sandy soil, poor in humus, is deprived of ground water and is dependent for its moisture solely on the atmosphere, the plants growing in it will be retarded in their development if rain and dew are absent for any length of time, and their outward appearance will be altered by this restriction of growth. Annual plants subjected to a lack of moisture in the soil just at the time when their growth should be at its maximum, show best how far these alterations will go. The stem-structures remain short, the foliage-leaves shrink to their smallest extent, and no lateral shoots are developed. Only a few, or perhaps only one, of the flower-buds mature; it is small, opens comparatively very early, and the whole plant has a dwarfed aspect. Annual plants of the Poppy (*Papaver Rhœas, somniferum*), Pheasant's Eye (*Adonis æstivalis, flammea*), Corn-cockle (*Agrostemma Githago*), Cornflower (*Centaurea Cyanus*), and common Groundsel (*Senecio vulgaris*) grown on a dry soil differ from plants grown in the same place, but in a damp year, to such an extent in the size of all their parts that at first sight they might be mistaken for other species. A clay soil which retains water is less exposed to danger of too great dryness, but if it is not mixed with humus, and therefore loosened, it has the disadvantage that the water it contains cannot take up the inorganic foods quickly enough and in sufficient quantity for the requirements of the plants. This drawback explains the surprising fact that plants grown on heavy wet clay soils have a dwarfed appearance exactly like plants growing on dry sandy soil. In regions liable to flooding by streams and rivers where not infrequently sandy and clay soils, in all degrees of porosity and admixed with humus in all possible proportions, are to be met with within a few yards of one another, certain species of plants are to be found growing near together in all imaginable degrees of size, e.g. *Aster Tripolium*, *Bidens cernua* and *tripartita*, *Polygonum lapathifolium*, *Rumex maritimus*, *Veronica Anagallis*. In places where the seedlings cannot find enough free mineral foods, in spite of the abundant moisture in the soil, the stem rises to some 3-8 cm.; in places which favour the absorption of food, to some 50-80 cm. We will describe only one species, *Veronica Anagallis*, more in detail. Plants of this species are found with stems 3-5 cm. high and 0.5 mm. thick, with foliage-leaves 6-12 mm. long and 5-6 mm. broad when fully developed. The number of flowers in one inflorescence is about 4-5, the calyx and ripe capsular fruit measure 3 mm. in length. Contrasting with these are plants with stem 30-50 cm. high and 7-8 mm. thick, whose fully-formed leaves are 80 mm. long and 35 mm. broad. There are 40-50 flowers in each inflorescence, and the calyx and ripe capsule measure 4-5 mm. in length. Generally speaking these plants are about ten times as large as the others. If the soils which give rise to such surprising differences in size are examined it will be noticed that the dwarfed specimens are rooted in a heavy soil devoid of humus, while the large luxuriant plants flourish in a clay soil which is mixed with plenty of humus, and is therefore very open. Obviously the plants could not obtain from the heavy clay soil what they required for the structure of a vigorous plant, even although the

ground was well moistened and warmed; but this they could obtain in abundance from the saturated clay soil containing the humus.

It has been already stated that the ground water is less favourable for vegetation than rain and dew on account of its paucity of carbonic acid. But the moistening of the ground by water which wells up from below brings other evils in its train. By this means the soil is over-saturated for a long time, a condition which the roots of most land-plants will not tolerate. When it remains stationary for a long while potassium and sodium salts, and, under certain conditions, humous acids pass into it from the wet earth in quantities anything but advantageous to the plants. Vegetation, therefore, exhibits a scanty growth in places where the ground water influences the stratum of soil penetrated by roots, and it usually consists of comparatively few species.

In low-lying regions, where the ground water rises to the surface, we have the formation of lakes and ponds with variable water-level. Sometimes the plants growing in such places are quite submerged, while at other times their stem and leaves are above water. Land plants do not take kindly to this. Most of them cannot survive very long immersion; they become suffocated, die, and decompose under water in a few days. Only a few species have the remarkable power of growing equally well below or above water, and these are, of course, extremely interesting on account of their form. In accordance with the great contrast presented by the external conditions of life to which these species are temporarily exposed we have a fundamental change both in their outward appearance and in the internal structure of their several organs. In order that the stem and leaves should be held in the best position by the flowing water, the mechanical tissue in submerged varieties of these species is much reduced (see vol. i. pp. 424 and 665). They are also devoid of the contrivances which usually regulate transpiration, since no evaporation occurs under water. Stems grown under water consequently appear limp and flaccid when taken out of it; their leaves, when compared with those growing in the air, are much weaker and more delicate. They have no gloss, but are brighter green in colour, and in the air they collapse and dry up in a very short time. A vertical section through the leaf shows that the number of cells between the upper and lower epidermis is much reduced, and that the cells are shortened in a direction perpendicular to the leaf surface. The foliage-leaves of *Veronica Beccabunga*, when grown under water, are hardly one-third as thick as those grown in the air, and between the upper and lower epidermis there are only 4-5 layers of short cells, while in corresponding leaves of aerial plants there are 10-12 cell-layers and a distinct division into palisade and spongy parenchyma (see vol. i. p. 279). The shape of the leaf is also much changed under water. In *Veronica Beccabunga* the difference in aerial and submerged leaves is very slight, consisting only in the shortening of the petiole and in the marginal teeth becoming less marked. In *Veronica Anagallis*, likewise, the alteration in shape is inconsiderable, but in many others it is very noticeable, and we shall return to it when speaking of the influence of light.

Plants rooted in the mud of a river-bed, the stems and leaves of which are surrounded by rapidly-flowing water, must possess corresponding strength if they are not to be torn. In comparing two plants of the same species, the one growing in the still water of a deep lake, the other in a rapidly-flowing stream, it will be noticed that the walls of the superficial cells of the latter have become strongly thickened, and that strong bundles of bast-fibres have developed in the cortex of the stem, while in the former only the weakest traces of bast-fibres can be seen. The extraordinary length of stem, petiole, and leaf-blade is also very surprising in plants which grow in rapid water. The Pondweed *Potamogeton fluitans*, the Rushes *Juncus lamprocarpus* and *supinus*, the Grasses *Agrostis stolonifera* and *Glyceria fluitans* are very instructive examples. A plant of the last-named Grass growing on damp soil on the edge of a stream over the water had linear, bluntly-pointed leaves, whose sheaths were on the average 15 cm. long, the blades 23 cm. long and 8.5 mm. broad. After this plant had been submerged under rapidly-flowing water in the following year, leaves unfolded, which tapered gradually to a point, with a sheath having a mean length of 47 cm., and blades 73 cm. long but only 5 mm. broad. The blades produced in running water were three times as long and actually rather narrower than in the air. There was no difference in the number of strands traversing the blade, but they were nearer to one another than in the aerial leaves. The Arrow-head (*Sagittaria sagittifolia*), which usually grows on the muddy bottom of shallow lakes, raising its leaves above the still water, has gained its name from the likeness of its leaf-blade to an arrow. If it is planted in the bed of a rapid stream so that the leaves during their development are exposed to a vigorous current, the leaf-blade is almost entirely suppressed. What still remains has the form of a spade, but not infrequently all trace of lamina is wanting. The petiole, however, lengthens to 70 cm., and forms a limp, flat, pale-green ribbon 1-2 cm. broad, which might easily be mistaken at first sight for the leaf of *Vallisneria*.

Another remarkable change which is effected by submerging growing plants is the non-development of the epidermal structures called hairs, so that the leaves and stems of submerged plants always appear smooth. The suppression of hair-structures is very noticeable in the aquatic variety of *Polygonum amphibium*. In aerial plants of this species the leaves have short petioles, are lanceolate in shape, and are covered thickly with short hairs, which are rough to the touch; while the aquatic plants have long-stalked, broadly-linear leaves completely smooth on both sides.

The humidity of the atmosphere has a marked effect on the form of land plants. Transpiration, which is so deeply concerned in all the vital processes, is carried on very slowly in air which is almost or quite saturated with water-vapour. If plants of a species which usually grows in dry air come into a humid atmosphere, they must be furnished with means for aiding evaporation. On the other hand, plants which grow in dry air must be protected against excessive transpiration. The aids and protective measures were so minutely described

in vol. i. pp. 284 and 307, that it is needless to repeat them here; but it should be noted that the capacity of plants to construct their tissue as need requires, either for aiding transpiration or for protection against excessive evaporation, is very limited. It must also be pointed out that it is very difficult to distinguish clearly between the direct effect of the humidity of the air and the effects of other influences. Heat and light, as well as the amount of moisture in the soil, are intimately connected with the humidity of the air, but the relations are difficult to estimate. To a certain extent they are interchangeable, and therefore, in most instances, it is impossible to say which external influence is the cause of any particular alteration in the tissue concerned in transpiration. For the answer to the chief question, whether it is possible for a change in the conditions of life to cause an alteration of form in the sense of an adaptation, it is really a matter of indifference which influence causes the visible effect. Only here, as in so many other cases, matters are simplified if a certain partiality is permitted in experiments for solving these difficult questions, and if the interwoven influences of soil and climate are treated separately.

The effect of heat on growing plants was discussed at vol. i. p. 523. It only remains to say here that the formation of starch and other reserve-foods, as well as the formation of sugar in fruits, is largely connected with heat. Fruits of the same species which ripen under a higher temperature differ greatly in the amount of sugar they contain from those ripening at a lower temperature. It is generally accepted that the size also of the stem, foliage, flowers, and fruit is influenced by heat. The changes which occur when plants in flower, after being for some time in a very warm room are transferred into a cooler room, the other conditions remaining the same, are in particular now recognized. When a large-flowered bulbous plant, *e.g.* the Belladonna Lily (*Amaryllis Belladonna*), is transferred to a cold greenhouse after opening its first flowers in a warm one, the flowers it here develops at a lower temperature are almost a third smaller than those produced in the warm house. But when the first flowers open in the cold, and the later ones in a warm atmosphere, the former remain small and the latter are larger in size. It is important to emphasize this circumstance in order that the phenomenon here exhibited may not be mistaken for another, in case we should be led to think that the flowers of a plant which first unfold are larger than those which succeed them even when there has not been the slightest alteration in the conditions of light, heat, humidity, &c.

It is particularly instructive, when examining the effect of heat on the form of a species, to compare plants grown in water of different temperatures but under conditions otherwise similar. In mountainous districts the springs on the same mountain slope have a different temperature according to their elevation, and yet the same species of plants may be found growing in springs at the foot and high up on the mountain. Let us take as examples plants of *Cardamine amara*, *Myosotis palustris*, *Pedicularis palustris*, and *Veronica Beccabunga*. These species grow at the foot of the Patscherkofel, near Innsbruck, in the bed

of streams with a mean temperature of 10.2°C ., but they also flourish in a stream above the tree-line, at a height of 1921 metres above the sea-level, known as the "Kreuzbrunnen". Comparing plants of the same species growing under the influence of these different temperatures, the following differences are to be noted:—Plants of *Veronica Beccabunga* growing in spring water at a temperature of 10.2°C . were 20–50 cm. high, and displayed 4–6 internodes between the bottom in which they were rooted and the level of the first inflorescences. The internodes of the stem were 60–120 mm. long and 5 mm. thick; the leaves springing from the middle of the plant were 40–60 mm. long, 20–25 mm. broad, and each of the flower racemes had 12–16 flowers. Plants growing in the spring water at a temperature of 4.2°C . were 10–15 cm. high with 4–6 internodes between the ground and the level of the first inflorescences. The internodes were 15–30 mm. long and 10–12 mm. thick, and each inflorescence had 12–16 flowers. *Cardamine amara*, *Myosotis palustris*, and *Pedicularis palustris* behaved similarly. There seemed to be no alteration in the form of the leaves and flowers; the corollas assumed a rather deeper tint in the Kreuzbrunnen; *Myosotis palustris*, which was 20 cm. high at the foot of the Patscherkofel, was 4–5 cm. high in the Kreuzbrunnen, and closely resembled the *Eritrichium nanum* of the Southern Alps in the deep blue of its corollas. *Cardamine amara*, in the same cold spring, in addition to the shortening of its internodes and diminution of its foliage-leaves, displayed a red colour on the outside of its white petals which was not present in plants at lower levels.

The powerful influence of light on the development of plants was discussed at vol. i. p. 371. The question now before us is how far bright and subdued light are able to alter the size, form, and colour of plants. The following is a general review of what has been ascertained in the matter from experiments and direct observation of nature. When plants of a species develop in subdued light they always have higher stems and longer leaves than when grown in bright light, provided, of course, that the conditions of moisture and temperature have been as far as possible identical. This difference is especially noticeable in comparing two plants of a species, one of which has developed in the dim light of a greenhouse in the short days of winter, the other in an unshaded place in the open country during the summer when the light lasts for 16–17 hours every day. The former has a lank thin stem, delicate yellowish-green leaves, and either none of its flowers unfold or else they have a weak appearance and their corollas are pale and flaccid. The illuminated plant has, on the other hand, a compact vigorous stem, dark green leaves, and unfolds a multitude of bright-hued flowers. One only of the large number of experiments which have been performed for the purpose of determining this matter definitely will be mentioned here—one indeed which shows how far the form of the flowers also may be affected. Seeds of a biennial Saxifrage, *Saxifraga controversa*, which were sown in several flower-pots filled with similar soil, produced numerous young plants. A pot with six of these young plants was taken in the autumn into the hot-house; another, likewise containing

six young plants, passed the winter under a thick coat of snow in the open. At the beginning of December the six plants in the hot-house sent up from the centre of their small leaf-rosettes slender stalks 10 cm. high, whose upper internodes were 22 mm. long and 1 mm. thick. The stem-leaves were yellowish, entire, elongated, 6-7 mm. long and 2 mm. broad; calyx-tube 4 mm. long, 13 mm. broad; calyx-teeth 2 mm. long, 1.5 mm. broad; petals 3.5 mm. long, 2 mm. broad; stamens 1 mm. long. It was noted that lateral axes only developed in the axils of the upper stem-leaves, and that the buds of the lateral shoots in the lower leaf-axils atrophied. In the following May strong stems 6 cm. high were sent up from the leaf-rosettes of the plants which had wintered under the deep snow in the open; their upper internodes were 12 mm. long and 2 mm. thick. The stem-leaves were somewhat broadened in front with dentate margin, red in colour, 5 mm. long and 3 mm. broad. The measurements of the parts of the flowers were:—Calyx-tube, 2 mm. long, and 2 mm. broad; calyx-teeth, 1.5 mm. long, 1 mm. broad; petals, 2.3 mm. long, and 2 mm. broad; stamens, 1 mm. long. From the axils of the stem-leaves flower-bearing shoots developed, which, like the parts of the main stem exposed to the sun, were coloured red. Here then the alterations which certainly are due to the various light influences consist not only in the lengthening and shortening of the stem- and foliage-leaves, but the flowers are correspondingly changed. The petals of the flowers which opened at the New Year when the days were shortest were not only relatively but actually narrower than those which belonged to flowers which opened in the early summer when the days were longest.

It has already been stated that the elongation of the leaves and the division of the leaf-lamina into long narrow segments in submerged leaves is associated with the diminution undergone by the light in passing through the water (see vol. i. p. 665). The elongation of submerged leaves is very well seen in the water Starwort (*Callitriche*) and Mare's-tail (*Hippuris*). In the latter the linear submerged leaves are thirty times as long as they are broad, while the length of the aerial leaves is only 7-9 times their width. In *Roripa amphibia* the leaves which develop under water are deeply cleft compared with those produced in the air. The aerial leaves of this Crucifer are linear-lanceolate, about ten times as long as broad, with finely toothed margin. Under water the leaves have an elliptical shape, are 2-3 times as long as broad, and the lamina is cleft almost down to the midrib in narrow segments 2-3 cm. long, like a comb or feather. The aerial leaves of the whorled Waterwort (*Elatine Alsinastrum*) are grouped in whorls of three. They have an ovate shape, and their margins are finely notched. Each is traversed by 3-5 veins. The leaves developed under water are divided almost their whole length into 3-4 narrow linear segments, and each whorl looks as if it were composed of twelve leaves. Each segment is smooth round the edge, and traversed only by one central vein. The difference between the aerial and submerged leaves of the white-flowered Crowfoots (belonging to the *Batrachium* section of the genus *Ranunculus*) is even more surprising. Plants of these Crow-

foots which have developed on muddy but not inundated ground display three- or five-cleft leaves whose segments are light green in colour, shiny, and almost fleshy, and spread out flat. When these plants are grown under water the leaves appear quite different; they become divided into numerous thread-like or hair-shaped segments which have a dark-green colour, and the polished surface has entirely disappeared.

The shade afforded by stones, loose earth, undergrowth, and neighbouring bushes and shrubs acts on growing stems, foliage-leaves, and flowers just in the same way as the light-subduing layer of water. In a place near my country house which was formerly used for storing wood and dry twigs, but which had remained unused for a long time, the Creeping Thistle (*Cirsium arvense*) had established itself and formed an intricate growth. The crowded stems attained a height of 80 cm. at the time of flowering and fruit ripening. In the winter of 1885 wood was again stored there in piles 150 cm. high. When, early in the following summer, the new shoots of the Thistle began to spring up they were obliged to content themselves with growing through the dark chinks between the blocks of wood. Many were thus forced to bend and twist, and finally came against some insurmountable obstacle so that they dwindled in the crevices of the wood-stack without ever reaching the light. Others again which were able to find a fairly straight road through the crevices grew up until they reached the surface of the wood-heap, they then continued to grow 50 cm. higher and unfolded large foliage-leaves on this upper portion. They also developed branches with flower-heads, and from a distance it looked as if a group of Thistles had grown on the top of the wood-stack. The stems had attained a height of 2 metres. The lower internodes were twice as long as usual, the foliage-leaves which sprang from the stalk inside the dark crevices were small, yellowish green, and the buds in their axils did not develop. The Cow-berry (*Vaccinium Vitis-Idaeae*) behaves similarly when its shoots are obliged to grow up to the light through dead tree-trunks. Shoots which force their way in the dark between the bark and the wood of the trunk may reach the height of a metre, while neighbouring ones, springing directly from the soil of the forest are only 15 cm. high. The shoots inside the bark have a reddish colour, and they bear small pale scales instead of dark-green foliage-leaves.

From the creeping stems of the White Clover (*Trifolium repens*) spring erect petioles terminating in three leaflets, and an erect angular stem bearing a flower-head. In sunny places, especially where no neighbouring plants cast a shade, the petioles reach a length of 8 cm., and the stem of 10 cm. But if dense bushes overshadow the Clover, the petiole and stem elongate until the leaflets and capitulum they bear reach the light. Under these conditions petioles 28 cm. long have been found, and stems attaining a height of 55 cm. An extraordinary elongation also occurs in the radical leaves of the Dandelion (*Taraxacum officinale*) in places where high Grasses and thick bushes shade the moist soil. In the open the leaves reach a length of 20 cm., but in the shade they become twice or three times as long. The lower part of the leaf lengthens most, the free end is comparatively

very little altered, and in the central portion the only change is that the lobes and teeth become shorter and less clearly marked.

In order to ascertain the effect of covering plants with earth, numerous bulbs of a species of Tulip (*Tulipa Gesneriana*) were planted at the same depth in one garden bed, and in another some corms of the Spring Crocus (*Crocus vernus*). Earth was heaped over these bulbs and corms in successive heights of 5, 10, 15, 20, 25, 30, 35, 40, 45, and 50 cm. Naturally the leaf-tips and flower-buds were first seen in the places where the bulbs were only covered with 5 cm. of soil; in both beds the development was delayed—in the other cases in proportion to the height of the soil above the bulbs. Some flower-buds of the Crocus appeared above the 20 cm. of soil, one of the Tulip above the 30 cm. Numerous leaf-tips of the Crocus appeared above the 35 cm., and a few of the Tulip above the 40 cm. of soil. The perianth-tube, the peduncle and the foliage-leaves were almost twice as long as those which had developed under only 5 cm. of soil. The flowers were smaller, and unfolded just above the soil; the leaves were narrower and pale yellow in colour as far up as they were covered with the soil. Neither the Crocus nor the Tulip raised their leaves higher than 40 cm. Apparently the reserve-materials stored in the corm and bulb-scales were not sufficient for a further elongation. The stems and leaves of the Crocus and Tulip thus exhibit alterations similar to those observed in the sprouts of Potato-tubers in a dark cellar.

We should expect that if moisture and lack of light produce elongation of shoots and various alterations in leaves, a brilliant illumination would have the opposite effect on growing plants. This is indeed the fact. Plants which have been for a year in the shade and have been placed at the beginning of their development in the following year in the sun display shorter internodes and firmer leaves: they blossom more abundantly, the flowers are of a deeper hue, and in many cases a covering of hairs is formed over the green portions. It is not necessary to mention how far transpiration, which is much more active in the sun than in the shade, is concerned in this: these alterations are certainly produced in the end by sunlight.

The effect of brilliant illumination is best seen by comparing plants grown from similar seeds at different elevations, but under identical conditions in other respects. The results obtained in my experimental garden near the summit of the Blaser in the Tyrol, at a height of 2195 m., during the years 1875-1880 illustrate this very fully, and I will briefly recount them here. The seeds of some annual plants were sown in September. The beds were covered with a layer of snow a metre thick throughout the winter. The germination of the seeds took place in the following year soon after the snow melted between the 10th and 25th June. The seedlings therefore developed during the time when the sun was highest and the days longest, and the young plants were exposed to a temperature not lower but rather higher than that enjoyed by plants from similar seeds which began to develop in the experimental beds of the Vienna Botanic Garden in March, when the daylight lasted about 12 hours. The seedlings of several species (e.g. *Gilva tricolor*, *Hyoscyamus albus*, *Plantago Psyllium*, *Silene Gallica*, *Trifolium incarnatum*) were

killed by the isolated frosts which occurred in each of the six years of the experiment, not only in the last week of June, but during July and August; but others (e.g. *Agrostemma Githago*, *Centaurea Cyanus*, *Iberis amara*, *Lepidium sativum*, *Satureja hortensis*, *Senecio vulgaris*, *Turgenia latifolia*, *Veronica polita*, *Viola arvensis*) only underwent a short temporary stoppage of growth from this cause, and opened their flowers at the end of August and beginning of September. In the plants of some species (e.g. *Senecio vulgaris*, *Veronica polita*, *Viola arvensis*) ripe seeds capable of germinating were formed in September. The flowering specimens, in comparison with those which had grown during the short days of the spring exposed to numerous night-frosts in the Vienna gardens, displayed extremely shortened internodes. The number of internodes was also lessened, or rather, fewer were developed. For example, where 10 internodes developed in an experimental plant in Vienna, in the Alpine garden a corresponding plant would only have 5-6. The same was true of the development of the flowers. While in a plant of *Viola arvensis* in Vienna the axillary buds of the first six foliage-leaves were suppressed and flowers were not produced until the seventh and eighth leaves, flowers grew from the third and fourth axillary buds in the same species of plant grown in the Alpine experimental garden. The number of flowers on a plant was less, the petals were smaller on the average, and, generally speaking, the annual plants in the Alpine garden had the same appearance as those grown in the plain on dry, sandy soil described on p. 500. It has already been stated on p. 453 that some of the species which are annuals in the valley and on the plain do not die in the autumn in the Alpine garden, but remain alive through the winter and in the following year develop new shoots from the stem.

To describe the alterations undergone by biennial species in Alpine regions we will take *Libanotis montana* (an Umbellifer) as an example. Its stem in the Alpine garden was 16-24 cm. high and developed 5 internodes which were 2-5 cm. long. From the axils of the 5 green stem-leaves sprang lateral shoots which did not branch but terminated in a single umbel, so that the plant only bore 5 umbels altogether. The plants grown from similar seeds in the Vienna Botanic Garden exhibited a stem more than a metre high with 10 internodes each 10-20 cm. long. No lateral shoots were produced from the axils of the lower stem-leaves. Those from the axils of the middle and upper leaves were branched and bore several umbels. On an average a plant had about 20 umbels altogether.

Over 300 species of perennial plants were grown in the Alpine experimental garden. Only 32 of them blossomed, however. Those whose flowers usually precede the foliage-leaves were in full blossom at the beginning of July, the others, which had to develop a leafy stem before their flowers appeared at the top or in the axils of the leaves of this stem, did not flower until the end of August and beginning of September. Three species of the latter kind will be more particularly treated of here; one species whose stem bears only a single leaf and is terminated by a single flower (*Parnassia palustris*), one whose stem is beset with decussate leaves and terminates in a loose inflorescence composed of small cymes (*Lychnis*

Viscaria), and a third whose stem bears alternate leaves and whose flowers are grouped in capitula (*Pyrethrum corymbosum*).

The Grass of Parnassus (*Parnassia palustris*) from the Alpine garden, when compared with plants grown in the experimental beds of the Vienna Botanic Garden, showed the following measurements:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of stem	20-27 cm.	5-9 cm.
Dimensions of leaf	3.3 cm. long, 2.4 cm. broad.	1.0 cm. long, 0.6 cm. broad.
Diameter of flower	2.8-3.4 cm.	1.8-2.0 cm.

In the Alpine regions, therefore, the plant was only $\frac{1}{3}$ or $\frac{1}{4}$ as high and the leaves only $\frac{1}{3}$ - $\frac{1}{4}$ as large as in Vienna, whilst the flowers in the Alpine region had a much smaller diameter than in Vienna.

Comparing the hermaphrodite plants of *Lychnis Viscaria* in the experimental garden of the Blaser with those of the same species at Vienna, we obtain the following:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of the stem, including } the axis of the inflorescence }	400-500 mm.	230-240 mm.
Dimensions of lower leaves	80 mm. long, 4 mm. broad.	50 mm. long, 3 mm. broad.
Inflorescence	80 " " 50 " "	60 " " 40 " "
Calyx	15 " " 6.5 " "	13.5 " " 5 " "
Lamina of petals	10 " " 8 " "	8 " " 6.8 " "
Claw of petals	8 mm. long.	7 mm. long.

Plants from the Alpine garden, therefore, when compared with those from the Vienna Botanic Garden, exhibit smaller measurements of stem, leaves, and flowers. The following points were also noted: the number of internodes in plants from the Vienna Garden was 9, of which 5 were on the axis of the inflorescence; each cyme consisted of 3-5 flowers, and the whole inflorescence bore 33-40 flowers. Plants from the Alpine Garden had only 6-7 internodes, of which 3 belonged to the inflorescence; the cymes composing the inflorescence were only occasionally 3-flowered; in most of them only the central flower developed, the two lateral ones being suppressed. The whole inflorescence included only 5-11 flowers.

Plants of *Pyrethrum corymbosum*, from the Alpine Garden, compared with those from the Vienna Botanic Garden (all raised from one batch of seeds) showed the following differences:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of the stem	950 mm.	250 mm.
Dimensions of leaves	170 mm. long, 50 mm. broad.	45-50 mm. long, 20 mm. broad.
Diameter of the capitulum	26 mm.	20 mm.
Ray-florets	8 mm. long, 4 mm. broad.	7 mm. long, 3 mm. broad.

In this case, again, plants from the Alpine Garden, when compared with those of the Vienna Botanic Garden, had smaller stems, leaves, and flowers. The lobes of the foliage-leaves from the middle of the stem of plants from the Alpine Garden were pinnate, and the pinnæ were either entire or beset with two small teeth on each side, near the apex. The stem had ten foliage-leaves, the four uppermost of which were much reduced and served as scale-leaves for the lateral shoots arising from their axils. These lateral axes were not branched, and each bore only a single capitulum. There were five capitula altogether. On plants from the Vienna Botanic Garden the lobes of the foliage-leaves from the middle of the stem were more divided, and the pinnæ were beset on each side near the top with 3-5 teeth. The stem bore 25-27 foliage-leaves, of which the 6-8 upper ones were much reduced in size, and functioned as scale-leaves for the lateral shoots in their axils. These lateral shoots were branched, and each branch terminated in a caputular inflorescence. The total number of capitula was 20-30.

From these examples it will be seen that all the parts of plants grown in the Alpine experimental garden were much hindered in their growth. The foliage- and floral-leaves were smaller, the stems shorter, the number of internodes, foliage-leaves, inflorescences, and flowers was diminished. The flowers were relatively nearer the earth, and this was due not only to the diminished number and length of the internodes of the stem, but principally to the fact that the flowers sprang from the axils of the lower stem-leaves.

Plants growing in Alpine regions derive a great advantage from these alterations, which are chiefly produced during their development by the influence of the long and bright daylight of June, July, and August. If these plants had to produce the same under-structure as their fellows in the Vienna Botanic Garden, 2015 metres lower down, much time would be lost, and the earliest flowers would hardly open before October, at a time when the winter snow is already beginning to fall. But since the number of internodes is restricted, and flowers are developed from the lower stories, it is possible for the plants to blossom at the end of August and beginning of September, and perhaps to ripen their fruits—one of the chief aims of the plant's existence. To this modification in their mode of development is also due in part the repeatedly-mentioned fact that many alpine plants blossom earlier than those in lower regions. But in order to avoid misunderstanding, it must be expressly stated that in not one of the thirty-two perennial, nor in the biennial and annual species which blossomed in the Alpine experimental garden, was the early flowering hereditary; consequently these plants must be carefully distinguished from the so-called asyn-gamic species, which will be spoken of in one of the last chapters in this book.

The relation of light to the colouring matters of plants has been repeatedly the subject of careful investigation. All observers agree that the amount of the pigment known as anthocyanin increases and diminishes with the stronger or weaker sunlight enjoyed by the parts of the plant in question, and that the yellow colouring matter of flowers holds a similar relation. Chlorophyll, however,

is actually destroyed by bright light in plants which are not properly screened, and the green tissue is then blanched and assumes a yellow tint. Since the intensity of the sun's rays increases with the elevation in mountain districts (see vol. i. p. 525), we should expect that this effect of light would be shown particularly well in plants of high elevation. And this is certainly the case. The flowers of species grown in the Alpine garden on the Blaser at a height of 2195 metres above the sea exhibited, as a rule, brilliant floral tints, and some were decidedly darker than the flowers grown in the Vienna Botanic Garden. *Agrostemma Githago*, *Campanula pusilla*, *Dianthus inodorus (sylvestris)*, *Gypsophila repens*, *Lotus corniculatus*, *Saponaria ocymoides*, *Satureja hortensis*, *Taraxacum officinale*, *Vicia Cracca*, and *Vicia sepium* are good examples of this. Several species, which produced pure white petals in the Vienna gardens, e.g. *Libanotis montana*, had petals coloured reddish-violet by anthocyanin on their under sides in the Alpine garden. The glumes of all the Grasses which were green, or only just tinged with violet at a low level became a dark brownish-violet in the Alpine garden. The abundant formation of anthocyanin in the green tissue of the foliage-leaves and sepals, and in the stem, was particularly apparent. The leaves of the Stonecrops, *Sedum acre*, *album*, and *sexangulare* became purple-red, those of *Dracocephalum Ruyschianum* and *Leucanthemum vulgare* violet, those of *Lychnis Viscaria* and *Satureja hortensis* a brownish-red, and the foliage-leaves of *Bergenia crassifolia* and *Potentilla Tirolensis*, even in August, had the scarlet-red colour which they usually assume in sunny spots in the valley in late autumn. I must not omit to mention that, according to some of my zoological friends, many animals, especially spiders and snails, which have been transferred from the plains to the mountain-heights, assume a darker tint in alpine regions.

A considerable number of plant species, especially those which grow in the valley in shaded or half-shaded places, as, for example, *Arabis procurrens*, *Digitalis ochroleuca*, *Geum urbanum*, *Orobis vernus*, *Valeriana Phu*, and *V. simplicifolia*, *Viola cucullata*, developed more or less yellowish leaves in the Alpine garden, where they were exposed to the full sunlight. It was mentioned in vol. i. p. 393, that the Flax (*Linum usitatissimum*), which flourishes in mountain valleys at a height of 1500 metres, where its chlorophyll is uninjured, nevertheless turns yellow in the Alpine garden at a height of 2195 metres.

From this general review of the modifications in plant-form obtained by culture-experiments, a series of important conclusions may naturally be drawn. In the first place we must point out that two kinds of characters are to be observed in plants, those which are the result of certain conditions and properties of soil and climate, and those which appear independently of these external influences. This distinction is so important that we shall illustrate it by two examples. The white Water-lily, *Nymphaea alba*, develops scale-leaves of ovate or lanceolate shape with no separation into petiole and lamina. The foliage-leaves, however,

have a rounded petiole and a disc-shaped lamina. These characters are always present whether the seed which produced the plant germinates in a deep lake or in the mud of a marshy meadow. In the marshy meadow the scale-leaves remain short, and the walls of their epidermal cells thicken in a remarkable way; the petioles of the aerial foliage-leaves become about a span long, and, in order to increase their resistance to bending, a strong layer of bast arises, the thickness of these bast-layers amounting to 0.17 mm. The walls of the epidermal cells are thickened, 5-9 layers of collenchymatous cells are formed under the epidermis with walls 0.07 mm. thick, and the air-spaces in the centre of the leaf-stalk are much narrowed. But if this species of Water-lily grows under water, the scale-leaves elongate into long and flaccid ribbons, and the petioles of the foliage-leaves continue to grow until their blades are raised to the surface of the water. According to its depth they attain a length of 30, 40, 50-100 cm. Resistance to bending is but little required by the petioles, which are surrounded by water, and the bast is therefore only slightly developed. The strings of bast which traverse the leaf-stalk are only 0.11 mm. thick, the walls of the epidermal cells are only half as thick as in the aerial leaves, only 3-5 layers of collenchyma are developed below the epidermis and the air-spaces in the centre of the leaf-stalk have a diameter of over half a millimetre. These petioles are consequently flexible, and cannot support the leaf-blade if taken out of the water. The general form of the scale- and foliage-leaves, the segmentation of the latter into petiole and blade, the configuration of the blade and the distribution of the bundles in it are all the result of internal forces due to the specific constitution of the protoplasm; but the thickness of the epidermal cells, the strength of the mechanical tissue, and the length of the leaf-stalk, are determined by the depth of the water-covering. The same thing is seen in the flowers; their structure depends upon the specific constitution of the protoplasm, but the size of the petals is determined by the temperature of the water.

The Meadow-grass *Poa annua* has a rapid growth; its haulms and leaf-sheaths are round, the leaf-lamina is traversed by seven strands, the lower branches of the inflorescence are single or paired but never whorled, and the spikelets of the panicle are much compressed and egg-shaped in outline. These characters are unalterable and are observed in *Poa annua* under all conditions. But when the haulms growing in the gardens in the plain project beyond the short upmost leaf the spikelets become 6-7-flowered, and have a pale green colour. When the plants become perennial in alpine regions the haulms bend towards the ground and remain so short that they do not reach above the highest foliage-leaf; the spikelets develop only 3-4 flowers, and their glumes are dark violet on the surface and brownish-yellow at the edge; thus these modifications are in relation to peculiarities of situation (in the plain and alpine regions) as effect to cause, and are to be ascribed to the influences of heat, light, and moisture, which act in various ways according to the situation.

These alterations are always to the advantage of the plant. They make the

individual more resistant, support and protect its organs, and render it possible for the separate parts to perform their work in spite of the necessarily altered conditions. They seem to have the task of keeping the plant alive under very different vital conditions, of promoting growth and the formation of offshoots and fruit with the smallest possible expenditure, and they may therefore be regarded as adaptations to the particular conditions of soil and climate.

The capacity for adaptation is of course founded in the specific constitution of the protoplasm, and is very different in different species. One species may adapt itself by appropriate alterations to the influence of bright light, submersion under water, a dry atmosphere, &c., while another cannot do so. If the protoplasm of the Flax (*Linum usitatissimum*) could manufacture as much anthocyanin in its green tissue as the Summer Savory (*Satureja hortensis*) it would blossom and ripen its fruits in alpine regions as this plant does, and would not succumb to the effect of the strong light. If the protoplasm of the Common Bent-grass (*Agrostis vulgaris*) were able to continue its constructive activity under water it would not perish as soon as it is submerged, but would maintain itself like the stoloniferous species (*Agrostis stolonifera*) by green stalks and leaves adapted to an aquatic habitat. In short, the adaptability of each species is restricted within definite limits which depend upon the specific constitution of the protoplasm and cannot be overstepped.

It is a matter of great import in the history of species whether modifications in form effected by change of soil and climate are transmitted to the descendants, and whether they can be inherited. This of course can only be ascertained by experiments, and by experiments in which all possible sources of error have been eliminated. This last remark is made advisedly, for the sources of error in such experiments are very numerous. I will briefly indicate two which interfered with some experiments I carried out in the years 1863 and 1864. It is not enough to be careful that the seeds sown in the prepared experimental beds are all from the same plant; care must also be taken to see that they are not the result of a hybrid cross-fertilization. Some seeds taken in 1863 from a plant of *Dianthus alpinus* growing in the Botanic Garden at Innsbruck, and sown in different soil in two experimental beds, produced plants in soil free from lime, which, in their external appearance, agreed with *Dianthus deltoides*. It seemed as if *Dianthus alpinus*, a lover of limestone rock, had become transformed into *Dianthus deltoides* when grown without lime. The seeds of the plant so like *Dianthus deltoides* were again sown in soil without lime, but the resulting plants no longer resembled this species; they showed themselves to be constant in their characteristics. The whole experiment with *Dianthus alpinus* was then repeated, but this time the plants on the clay soil without lime did not change, and I was obliged to conclude that the plant I had regarded as a stage in the transformation of *Dianthus alpinus* into *Dianthus deltoides* was a hybrid of these two species. In order to be certain about this a crossing between the two species was effected artificially. From the resulting seed plants were actually grown which were exactly like those I had regarded as transformations, and there was no longer any doubt that some of the

stigmas of the *Dianthus alpinus* which had yielded the seeds for the first experiment had been pollinated by insects with the pollen of *Dianthus deltoides*.

Mistakes often arise also from the fact that the young stages of many plants are very different from the fully-grown specimens. Young Birches grown from the seeds of *Betula verrucosa* bear leaves which are simply serrated, thickly covered with hairs, and soft to the touch. They are deceptively like the leaves of adult plants of *Betula alba* or *pubescens*. The leaves of the adult *Betula verrucosa* have quite a different form; they are doubly serrated, smooth, and harsh to the touch. These latter are the only form of leaf described in Botanical books for *Betula verrucosa*. Anyone sowing the seeds from a grown tree, and watching them grow up, with leaves of a different shape and surface, might easily think an actual fundamental change had occurred, and might be tempted to regard the transformation as the direct effect of a change in external influences.

It is perhaps superfluous to state that due regard was paid to these possible sources of error in the later series of cultural experiments, carried out during six years in the Alpine garden on the Blaser (2195 metres), and for comparison in my Villa Marilaun in the high-lying Tyrolese Gschnitzthal (1215 metres), in the Botanic Garden at Innsbruck (569 metres), and in the Botanic Garden of the Vienna University (180 metres); *in no instance was any permanent or hereditary modification in form or colour observed.*

Seeds of a plant grown in the valley when sown in the Alpine region produced plants which exhibited the modifications described above. They were also manifested by the descendants of these plants *but only as long as they grew in the same place as their parents*. As soon as the seeds formed in the Alpine region were again sown in the beds of the Innsbruck or Vienna Botanic Gardens the plants raised from them immediately resumed the form and colour usual to that position. The modifications of form and colour produced by change of soil and climate are therefore not retained in the descendants; the characteristics which appear as the expression of these changes are not permanent, and the individuals are to be therefore regarded as varieties, of which Linnæus says in his *Philosophia Botanica*: "Varietates tot sunt, quot differentes plantæ ex ejusdem speciei semine sunt productæ. Varietas est Planta mutata a caussa accidentali: *Climate, Solo, Calore, Ventis*, &c., reducitur itaque in *Solo* mutato."

THE INFLUENCE OF MUTILATION ON THE FORM OF PLANTS.

When Birches and Firs grow up side by side in a wood-clearing, the crowns of the Birches will overtop the Firs in some twenty years' time, and this will seriously interfere with the growth of the latter. With every blast of wind the whip-like branches of the Birch strike against the upper shoots of the Firs, so that these gradually wither and die off. A lateral branch of a Fir tree altering its direction of growth and replacing the dead leader will, in its turn, soon be scourged to death. The top of the Fir is permanently mutilated, and the injury

can be recognized years after by the flattened form of the crown, so different from the usual appearance, when the offending Birches have perhaps long disappeared. Many other trees wage the same war with one another, the result in each case being the mutilation and alteration of the form of the summit of one of the trees. The Maple, for example, is either put quite *hors de combat* by the long thorny branches of a neighbouring *Gleditschia* (*Gleditschia triacanthos*) or else the crown becomes lop-sided owing to the destruction of the branches on the side facing the *Gleditschia*.

The way in which the appearance of Firs, Larches, Beeches, and Ling is altered by the attacks of ruminants, especially goats, was described in vol. i. p. 445, and we may add here that Pines and Junipers are mutilated in the same manner. The consequence is that lateral branches, which would not otherwise develop, grow out in the following year from the base of the twigs which have been bitten off. Apparently no other alteration takes place in these plants. But when huge boughs are broken off close to the ground by storms and the weight of snow, when the tree-trunks of the forest are sacrificed to the wood-cutter's hatchet, and the stems of seedling trees and shrubs in the meadow to the mower's scythe, when all the young shoots are frozen by a night's frost in spring, or when all the leaves are devoured by caterpillars and the branches are left bare as in winter—then the consequences are much more serious. In these cases new shoots make their appearance either from "eyes" in the stem or from the reserve-buds of the branches and twigs, or by buds produced by the roots below the ground. The leaves of these shoots, or *suckers*, as they are called, differ very much from those of the branches which have been broken, eaten, cut, or frozen off. The leaves from the crown of the Aspen (*Populus tremula*) are stiff and smooth in their adult condition; the circular blade is borne on a long petiole, and its margin is coarsely notched and undulated. The lateral veins traversing the blade are lost in a network near the edge in which no strong curved ribs occur. The leaves of a sucker from the base of a mutilated stem, or from the root, are soft and thickly covered on both sides with downy hairs; the heart-shaped blade is borne on a short stalk, and the margin is beset with numerous upwardly-directed notched teeth. The lateral veins of the blade merge near the edge of the leaf into a network, in which strong curved ribs are plainly visible. The leaves from the crown of the Oak (*Quercus pedunculata*) are deeply lobed and furnished with two so-called auricles at the base; those of the suckers are quite entire or very slightly lobed, with no auricles at the base. The leaves of the sucker of the common Beech (*Fagus sylvatica*) are more or less plainly serrated at the edge, while those of the topmost branches of the tree are quite entire. In the Black Mulberry (*Morus nigra*), and in the Paper Mulberry (*Broussonetia papyrifera*), the leaves of the sucker have a sinuous margin and are more or less deeply lobed, but those of the tree-top are heart-shaped with notched margins and no lobes. The leaves of the sucker of the Birch (*Betula verrucosa*) are simply serrated, with velvety hairs; those on the crown of the tree are doubly serrated and

smooth. The leaves on the suckers of the Round-eared Willow (*Salix aurita*) are broadly ovate, fairly smooth, and the veins in the blade form a wide-meshed reticulum; the leaves on non-mutilated branches are widened in the upper third, strongly wrinkled, and covered with grey hairs, whilst the reticulum of the veins is narrow-meshed. In *Salix rosmarinifolia*, the leaves of the suckers are twice or three times as broad as those of the normal branches, and they are smooth, while those of ordinary branches are covered with silky hairs, and gleam like silver. Hundreds of trees and shrubs might be mentioned in which there is a distinct difference between the foliage of the suckers and of the normal branches of the crown. But these few examples will suffice, and we will only mention the Norway Maple (*Acer platanoides*), because the difference in the foliage-leaves can be seen from the illustrations in vol. i. The leaves of the summit (see vol. i. fig. 106, p. 416, and fig. 109, p. 419) are borne on long petioles, the blade is 5-7 lobed, and the lobes are short and beset with several pointed, tapering teeth. The leaves of the suckers in this same Norway Maple are short-stalked, the blade is slightly 3-lobed, and each lobe is triangular and without the elongated pointed teeth. They exactly resemble the first foliage-leaves shown in vol. i. p. 9, fig. 1³. This is also true of the leaves on the suckers of other woody plants. The shoots developed from reserve buds, "eyes", and the like, repeat to a certain extent the beginning of the leafy stem, so that the phenomenon is only an exhibition of the usual metamorphosis of the foliage-leaves. The difference between the older and younger, *i.e.* lower and upper foliage-leaves, only seems strange because the two kinds of leaf-forms are not usually seen simultaneously on one and the same plant. By the time the crown of a tree has developed, the first (oldest) leaves which adorned the young sapling have long disappeared. Many descriptive Botanists, as a rule, only consider the foliage-leaves of the fully-grown trees and bushes; some of them have hardly ever seen the first leaves of the commonest trees, and when they do happen to come across them they regard them as an extraordinary phenomenon, declare the shoots bearing them to be "bud variations", and draw bold and bewildering hypotheses from their appearance. This alteration in form, however, has nothing to do with the formation of varieties, nor is it dependent either upon the influence of the soil or upon the effect of climate. Moreover, the form of leaf characteristic of the sucker is not possessed by the secondary shoots which arise from the suckers; these are adorned with the same foliage which occurs on the topmost branches of the tree.

Alterations in the scale-leaves as well as in the foliage are brought about by mutilation of the branches. When the upper portions of Willow boughs with their foliage-buds are cut off, leaving the lower portions with the buds of the flower-catkins on them, the small pale scales at the base of the catkins change into green foliage-leaves; the axis bearing these leaves elongates, and the catkins then form the termination of a leafy shoot. Many Willows, *e.g.* *Salix cinerea* and *S. grandifolia*, by this metamorphosis assume a very unusual appearance. In the following year the branches bearing the flower-catkins, if they are

not mutilated afresh, will again put out short catkin-stalks with small pale scales.

Mutilation of herbaceous plants is caused by herbivorous animals, viz. insects and mammals, and on a large scale by man when he mows the meadows and cuts the crops and makes other necessary invasions on the natural vegetation in the interests of husbandry. The alterations caused by these mutilations of the foliage-leaf region are in the main the same as in woody plants. From the remaining stumps of the stem lateral shoots arise whose first leaves are like the first leaves of the seedling. Usually they are less divided and have fewer hairs than the leaves on shoots of normal plants, and on this account they have a very different character. In the floral region the effects of mutilation are twofold—first the peduncles or the lateral axes which are terminated by inflorescences elongate, and then the flowers become smaller. For example, when a vigorous stalk of the Ox-eye Daisy (*Chrysanthemum Leucanthemum*) bearing a capitulum is cut off close to the ground, long lank lateral stems develop from the axils of the lowest remaining leaves, each one ending in a capitulum. The main stem is now seen to be branched at its base, which is never the case in normal plants. If about half the stalk of the common Foxglove is cut off in the spring long flower-racemes will arise from the axils of the leaves just below the cut, but the flowers will be only half as large as those which would have developed on the uncut main stem. The stem of *Althaea pallida* rises a metre above the ground if its development is not hindered, and forms fascicles of short-stalked flowers in the axils of the upper leaves. If the stem is broken off lateral axes develop from the axils of the remaining leaves, and bear little long-stalked flowers. Particularly good examples are furnished by the annual weeds *Delphinium Ajacis*, *Nigella arvensis*, *Stellera Passerina*, and the like, which grow up amongst cereals. Their main stems are broken off when the corn is cut, and they then develop comparatively long branches with small flowers from the remaining stumps. If only single flower-buds, and not the whole inflorescences, are removed from a herbaceous plant whose main stem terminates in a long raceme, so that each flower is cut away in turn from below upwards just before it opens, the rachis of the raceme elongates enormously and flower-buds are developed at its end which would certainly not have unfolded had there been no mutilation. In the Red Foxglove, for example, the rachis of the raceme which has been damaged in this way will grow to twice its ordinary length, and twice as many flowers will be developed. The last and highest flowers in such racemes, however, are only half the size of those which arise on normal racemes.

We must now consider certain perennial meadow plants which when mown down are stimulated by the mutilation to develop flower-stalks in the same year, which would, in the normal course of things, not have flowered till the year following. In Alpine valleys it is a very common thing for the flowers of the spring plants *Anemone vernalis*, *Geranium sylvaticum*, *Gentiana verna*, *Polygonum Bistorta*, *Primula elatior* and *P. farinosa*, *Trollius Europaeus*, &c., to appear in

the autumn in meadows which have been mown in the spring. The flowers appearing under these circumstances are remarkable for their small size. Their diameter is at least a third smaller than that of the spring flowers. In conclusion we may refer to the gardener's artifice which has already been described (p. 453) of producing perennial plants with woody stems from an annual Mignonette plant by mutilation. We might also mention the dwarf shrubs and trees produced by combined mutilation and grafting, especially the strange-looking little Ivy trees obtained by grafting a flowering branch of Ivy on an erect stem a span high, and the dwarf Conifers so much in favour with the Japanese.

Gardeners and descriptive Botanists have frequently determined and described mutilated plants as other species, hybrids, or varieties. They are neither the one nor the other. The peculiar appearance of the altered members resulting from mutilation is exactly determined beforehand in each species: it is due to the specific constitution of the species, and thus is part of its being. It is not produced by the external influences which lead to the formation of varieties, but is brought about by inherent necessity quite independent of the influences of climate and soil.

ALTERATION OF FORM BY PARASITIC FUNGI.

A considerable number of the trees and shrubs of Central and Southern Europe bear bristling, much-branched structures on some of their boughs which, from a distance, look like large birds' nests or brooms, and which have been popularly termed "witches' brooms". They are the outward and visible signs of a disease from which the plants in question suffer, and, as their name testifies, their origin was thought to be connected with witches. Traditionally witches have the power of "wishing" harm to mankind, animals, and plants; and superstitious people, at the sight of these peculiar pathological structures on the trees, may have started the idea that the disease was caused by witches that they might have brooms ready at hand for their midnight ride on the Brocken. Other plant diseases have been ascribed to unusual conditions of weather, especially to long-continued rain or great drought. It is not long since the discovery was made that most of the diseases attacking trees, shrubs, and herbs are caused by Fungi, and that atmospheric conditions are only concerned in the matter in so far as they hinder or favour the establishment and development of these parasites.

All the Fungi in question are parasites. They penetrate into the tissues of the host-plant and sooner or later cause the death of the affected part, and frequently of the entire host-plant. The living protoplasm in the cells and tissues of the host which is influenced by the parasite undergoes fundamental changes in its composition. Some of the cells are drained, their living protoplasm being consumed, so to speak, and these cells are obviously marked for destruction. Others are not killed, but changed. The metamorphosis occurs, in the first place, in the constitution of the living protoplasts which have not yet completed their development, the change much resembling that known as fermentation in fluid substances

(cf. vol. i. p. 508). In fermentation the chemical composition of the fluid is altered, its chemical compounds are shaken, decomposed, and split up and new compounds are formed by the action of the living Yeast cells. The same thing happens here in the interior of the living plant in its turgid, meristematic tissue—that is to say, in a group of protoplasts which still have the power of growing at the expense of materials supplied them, of increasing in size, and of multiplying by division. But these cells no longer behave as—in the absence of the parasite—they would have done. Profoundly modified under the influence of the parasite, but yet not killed, these cells, by their continued division, form tissues and organs of new and unusual form; in other words, that part of the host which is invaded but not killed by the parasite will continue to grow and increase in size, and in consequence of the change which its protoplasm has experienced will assume a different outward form.

These altered tissue-bodies produced by parasitic Fungi are called *gall-structures*. They are usually characterized by an excessive growth known as hypertrophy, as well as by their altered shape. The hypertrophy is without doubt caused by a stimulus proceeding from the parasite. We may conclude that the significance of the increased growth lies in the abundant supply of nourishment thus placed at the disposal of the parasite, since the large quantity of food-material brought for the excessive development of the hypertrophied growth connotes a large supply for consumption by the parasite. In many cases, however, the hypertrophied tissue merely forms a wall protecting the host against the further depredations of the intruder. It then contains no nourishment for the use of the parasite, being built up chiefly of corky cells, which the latter cannot consume or destroy. Such a tissue might be compared to the so-called callus which grows up in plants in parts deprived of epidermis after an injury, or in other wounds, and gradually covers them over with a protective layer.

The formation of the gall is often restricted to only a *small portion* of the afflicted plant: in other cases *whole leaves* and *branches*, and sometimes even *extensive shoots*, become modified in shape. To get a general idea of the four types of hypertrophied growths it will be best to take them one after the other in the order mentioned, commencing with the simplest.

The simplest of these galls consist of a few degenerate and metamorphosed cells in the centre of an extensive and unaltered tissue. They are produced chiefly by parasites of the genera *Rozella*, *Synchytrium*, *Exobasidium*, and *Gymnosporangium*. *Rozella septigena*, one of the Chytridicæ, develops swarm-spores which attack the various species of the fungal genus *Saprolegnia*. They settle on the tubular branches of the *Saprolegnia* at a place where it was just about to divide and to produce swarm-spores of its own. In consequence of the invasion of the parasite this does not take place, but the tubular cells which would have formed a *Saprolegnia*-sporangium divide instead into short barrel-shaped cells, each of which becomes a sporangium of *Rozella septigena*. In addition to this the infected cells develop lateral outpushings which swell up spherically, and each contains a resting-

spore of the parasite. Parasitic species of *Synchytrium* cause a vesicular enlargement of single cells of the epidermis in the leaves of phanerogamic host-plants. The not uncommon species *Synchytrium Anemones* and *S. Taraxaci* produce only a slight overarching, and the enlargement of the cells is hardly more than four times, often only twice the usual size. But, by the influence of *Synchytrium Myosotidis*, hypertrophied epidermal cells rise up from the leaves of the Forget-me-not (*Myosotis*) in the form of comparatively large, club-shaped, bottle-like, or egg-shaped bladders of golden or reddish yellow colour, and each contains the parasite, or rather its spores. The parts of the leaf attacked by *Synchytrium Myosotidis* are also much thickened, the palisade cells and the air-containing lacunæ of the spongy parenchyma (*cf.* vol. i. p. 279) disappear, and the tissue consists entirely of large similarly-shaped cells which fit close to one another, leaving no spaces between. In the gall caused by *Synchytrium pilificum* on *Potentilla Tormentilla* the much-enlarged cells in which the parasite settles are overgrown by the adjoining hypertrophied cells, some of which rise up in the form of hairs, and the whole new structure resembles a hairy wart.

A curious gall is produced by *Erobasisidium Rhododendri* on a sharply-defined portion of the *foliage-leaves* of the Alpine Rose (*Rhododendron hirsutum* and *ferrugineum*). A spherical spongy body rises from a restricted portion of the leaf, usually from the under side of the somewhat projecting midrib, sometimes only as large as a pea, sometimes as big as a cherry, and occasionally even attaining the dimensions of a small apple. It is yellow, but rosy-cheeked like an apple on the side turned to the sunlight, and it reminds one of this fruit by its succulent tissue and sweet taste. Indeed, these galls are sometimes called "Alpine Rose-apples". Their surface is covered with a bloom which is caused by the numerous spores developed there and does not consist of wax like the bloom on an apple rind. The neck joining the gall to the leaf is not more than 1-2 mm. across, and, what is still more remarkable, except for this sharply-defined place of connection the infected leaf is unaltered.

Galls produced by the Gymnosporangia on the leaves of the Mountain Ash, Pear-tree, Rock-medlar, and other Pomeæ exhibit strange forms. One of them, caused by *Gymnosporangium conicum*, on the foliage of the Rock-medlar (*Aronia rotundifolia*), is represented in fig. 357². It resembles a tubercle furnished with horns projecting from the lower surface of the leaf. Microscopic examination shows that the knob consists of the strangely metamorphosed spongy parenchyma of the leaf. The intercellular spaces which normally contain air are quite filled with the mycelial threads, and in the projecting portion of the tubercle, which is very hard and almost cartilaginous, tubes are inserted which terminate blindly below, where the spores of the parasite are developed, whilst above they are open and fringed, thus allowing the spores to escape. These tubes look like horns to the naked eye. Usually several galls occur together on the same leaf. They are conspicuous at some distance on account of their colour. The chlorophyll is destroyed wherever the mycelium of the parasite extends and a reddish-yellow

colour takes its place, so that orange spots appear on the surface of the foliage, contrasting vividly with the green of the unaltered portions of the leaf.

Galls rising from sharply defined parts of the *stem* are comparatively rare. One of the most remarkable is produced on the stems of a Laurel (*Laurus Canariensis*) by the parasitic *Exobasidium Lauri*. When it appears above the bark it looks like an aerial root, but rapidly grows into a branched spongy body 8-12 cm. long similar in appearance to one of the Fungi belonging to the family Clavariaceæ (cf. fig. 195¹, p. 21). The galls produced by *Entyloma Aschersonii* and *Magnusii* on the Composites *Helichrysum arenarium* and *Gnaphalium luteo-album*



Fig. 357.—Fungus-galls.

¹ Gall on the stem of the Juniper (*Juniperus communis*) produced by *Gymnosporangium clavariæforme*. ² Gall on the leaves of *Aronia rotundifolia* produced by *Gymnosporangium conicum*.

take the form of outgrowths, varying from the size of a pea to that of a walnut, developed from special spots on the root. Whether the spherical tubercles growing on the root-fibres of many Leguminosæ, especially those of the Bird's-foot Trefoil (*Lotus corniculatus*), the Fenugreek (*Trigonella fœnum-græcum*), Lady's-Fingers (*Anthyllis Vulneraria*), Lupin (*Lupinus variabilis*), and the Liquorice (*Glycyrrhiza glabra*) are to be regarded as true galls caused by the Bacteria-like organisms invariably to be found in their interior is questionable. According to the most recent investigations they are the outward expression of a case of symbiosis and not of pure parasitism.

Gall developments which involve whole roots or rootlets are found on the Alder (*Alnus glutinosa*), and on the Cabbage (*Brassica oleracea*). The gall which is produced on Alder roots by *Frankia Alni* attains the size of a walnut and has a

curious gnarled appearance; all the fibres of the root-branch thicken in a club-like or tuberous manner and become twisted and entangled with one another. The so-called "Fingers and Toes", caused by the Myxomycete (*Plasmodiophora Brassicae*), is a gall-like hypertrophy on the root of *Brassica oleracea*, which not uncommonly grows to the size of a man's head.

Many woody plants have galls which alter the internal structure as well as the outward appearance of large tracts of the stem. The parasites settle in the cortical parenchyma, producing hypertrophy there, and afterwards the most varied distortions and alterations in the wood of that region of the stem. The trunk, branch, or twig becomes much swollen or knotted and the cortex rent and torn. Resin or a gummy mucilage sometimes runs out of the rifts in the gall. As such a parasite exercises its metamorphosing faculty for several years, the canker (as it may be termed) increases in size continually. Sporangia of varied form and colour appear annually on the affected places, and again disappear when they have shed their spores. The part of the stem or branch above the cankerous cushion dwindles and dies off sooner or later. It rarely happens that the tree or shrub is able to rid itself of the parasite. Occasionally a growth of wood and cork from the adjoining healthy part walls in the cankerous spot so that the parasite is destroyed. The gall produced by *Gymnosporangium clavariaeforme* on the trunks and branches of the common Juniper (*Juniperus communis*) is an example of this form (see fig. 357¹). From the hypertrophy there project in the early spring golden-yellow tongues (shown in the figure) consisting of masses of spores embedded in mucilage. Other similar growths are produced on species of Juniper by *Gymnosporangium conicum*, *G. Sabinae*, and *G. tremelloides*, but it would take too long to describe their differences in detail. It is important to mention, however, that each of these parasites has two stages of development, living on different hosts, the hypertrophies as well as the associated spore-producing organs of the parasite being different in the two cases. The "Æcidium stage" produces cartilaginous swellings (see p. 520) in definite spots on the foliage of various Pomeæ (*Aronia*, *Crataegus*, *Pyrus*, *Sorbus*), the "Teleutospore stage" thickenings and tuberous outgrowths on the trunks of Junipers (*Juniperus communis*, *excelsa*, *Sabina*), and these parasites can travel from one host to the other in turn. (The two stages on different hosts are shown in fig. 357; these are not of the same fungus, but of nearly allied ones, and illustrate the point mentioned.)

The parasite *Peziza Willkommii* attacks the trunks and branches of the Larch (*Larix Europaea*), and produces the well-known Larch-disease or "Larch-canker". The parasite having gained access at some point on the stem or branch first penetrates the cortical parenchyma, and affects the cambium so as to prevent the further development of wood in that place. The development of the wood on the opposite side of the stem, *i.e.* the formation of annual rings, may proceed for several years, and in this way the attacked spot on the trunk takes the form of a depression, which is rendered the more conspicuous should the wood and cortex surrounding the parasite have undergone a greater thickening than usual. In

time the patch becomes a sunken, blistered hole from which resin flows; and every year the fructifications appear above the cortex in the form of numerous little cup-like structures which are white outside and scarlet-red in the concavity. As the disease progresses the infected patch gradually spreads, and infected trunks and branches can be easily distinguished at a distance. Towards the end of summer the needles on the twigs above the canker turn yellow, while those on the healthy branches are still a beautiful green. This premature discoloration is a sure sign of the speedy death of the whole bough. A similar canker is produced on the



Fig. 358.—Various Galls.

¹ Gall on the bract-scales of the pistillate flowers of the Gray Alder (*Alnus incana*) produced by *Exoascus Alni-incanae*.

² Inflorescence of *Valerianella carinata*. ³ The same inflorescence with galls produced by a gall-mite. ⁴ Leaf rosette of the House-leek (*Sempervivum hirtum*). ⁵ Leaf rosette of the same plant which has been attacked by the fungus *Endophyllum Sempervivi* and has become hypertrophied.

Silver Fir (*Abies pectinata*) by *Eridium elatinum*, but instead of being only on one side of the branch, as in the Larch, it forms a uniform swelling all round it. Cankers of this kind are produced by a Bacterial organism (*Bacillus amylovorus*) on fruit-trees (Apple, Pear, &c.), and on various trees belonging to the Amentiferae (Beeches, Hornbeams, Oaks, &c.) by the Fungus *Nectria ditissima*.

When *whole leaves* undergo hypertrophy of the kind we have particularly remarkable changes of form. For example, the normal leaves forming the rosettes of the House-leek (*Sempervivum hirtum*; see fig. 358⁴) are broadly obovate in form, being little more than twice as long as they are broad. The leaves of the same plant after they have been attacked by the parasitic *Endophyllum Sempervivi*

vivi (see fig. 358⁵) are seven times as long as broad and linear in shape. They stand erect, and are of a much paler colour than the healthy leaves. The Wood Anemone (*Anemone nemorosa*) affords another example (see fig. 259, p. 229). It spreads by creeping stems under the surface of the ground, and forms small colonies in light thickets and in meadows. The plants consist partly of flowering lateral shoots, and partly of foliage-leaves, which emerge above the ground from the creeping underground stem. In normal leaves the erect petioles are all the same length, and the leaflets are extended at about the same level. But when the *Æcidium* stage of *Puccinia fusca* has settled on them this becomes altered. The blades of the infected leaves tower over their healthy neighbours in consequence of the elongation of their petioles, whilst their leaflets are smaller and less divided. The length of the petiole in normal leaves is some 12–13 cm., in hypertrophied leaves 15–18 cm.; but the size of the altered segments, compared with those of normal leaves, is as 5:7. Similar changes are observed in leaves of *Soldanella alpina* when attacked by *Puccinia Soldanellæ*. The petioles of the infected leaves are 2–4 times as long as the normal ones, the blade is smaller and hollowed like a spoon instead of being flat, and the colour is an ochreous yellow instead of a dark green. The same alterations in the length of the petiole, and in the size and colouring of the leaf-lamina, are produced in the leaves of *Alchemilla vulgaris* by *Uromyces Alchemillæ* and in those of *Phyteuma orbiculare* by *Uromyces Phyteumatum*. To this class belongs also the so-called “curl” disease of Peach and Almond trees, produced by *Exoascus deformans*, and rendered conspicuous by the considerable enlargement, undulation, and bladder-like expansion of the infected leaf-surface, which acquires generally a very brilliant coloration.

Floral-leaves are comparatively seldom metamorphosed by Fungal parasites. In the Alder (*Alnus glutinosa* and *incana*) the bracts of the pistillate flowers are changed by *Exoascus Alni-incanæ* (= *E. amentorum*) into elongated purple-red spatulate lobes much twisted and bent (see fig. 358¹); *Peronospora violacea* sometimes causes the stamens to change into petal-like structures in the flowers of *Knautia arvensis*, so that they then seem to be “double”; *Ustilago Maydis* causes a growth of tissue in the pistillate flowers of the Maize, the result being that instead of grains irregular cushion-like structures 7 cm. in diameter are produced. *Taphrina aurea*, which settles on the pistillate flowers of Poplar (*Populus alba* and *tremula*) causes the ovaries to form golden-yellow capsules more than twice the usual size. The galls produced by *Exoascus Pruni* on the ovaries of wild Plum, Bullace, Sloe, and Bird Cherry (*Prunus domestica*, *insititia*, *spinosa*, *Padus*) belong also to this class. The tissue of the ovary increases in size, but not in the same way as in fruit formation. The resulting body is flattened on two sides, brittle and yellow; the seed inside is abortive, and a hollow space is left in its stead. The gall produced from the ovary of *Prunus domestica* has the form of a rather curved pocket, which looks as if it had been powdered outside with flour at the time the spores ripen. These hypertrophies, which are popularly termed “pocket-plums”, “bladder-plums”,

&c., fall off the trees at the end of May. They are eaten in many districts, but have an insipid, sweetish taste.

Galls consisting of *whole shoots*, both the stem and its leaves being altered by the parasite, are found principally on trees and shrubs, and only rarely on herbaceous plants. Examples of the latter, however, are furnished by the metamorphosed shoots of the Shepherd's Purse (*Capsella Bursa-pastoris*) produced by *Cystopus candidus* and *Peronospora parasitica*. Here the leaves, especially the floral-leaves, as well as the ground-tissue of the stem undergo pronounced hypertrophy. The petals, which measure only 2 mm. in length in a healthy plant, may become even 15 mm. long; the sepals also elongate, become fleshy and brittle, and are distorted and crumpled in all manner of ways. Only six stamens are developed in normal flowers, but in hypertrophied specimens there are often eight. The metamorphosis produced by *Uromyces Pisi* in one of the Spurges, *Euphorbia Cyparissias*, is even more remarkable. The stem elongates far beyond its usual dimensions, and the leaves, which are crowded together on normal shoots, are thus separated by considerable intervals. The distance between two adjoining successive leaves in the healthy *Euphorbia Cyparissias* is only 0.5 mm., but in the hypertrophied specimens it becomes 2-3 mm. Infected shoots on an average are twice as high as healthy ones. The foliage-leaves, which are thin, flexible, linear, and twelve times as long as they are broad in the healthy plant, become, in the infected specimens, thick, brittle, elliptical, and only 2-3 times as long as they are broad. The bluish-green colour of the normal plant is changed into a yellow-ochre tint, and this contributes not a little to the odd appearance of the plant. Affected plants are not uncommon in Switzerland; a locality in which this disease has been very prevalent in recent years being Saas-Fée in the Saas-thal. The metamorphoses produced on the shoots of Periwinkles (*Vinca herbacea*, *major*, and *minor*) by the Uredospore-stage of *Puccinia Vinca* and on shoots of *Cirsium arvense* by the Teleutospore-stage of *Puccinia suaveolens* are very like those of the *Euphorbia* just mentioned, since the stem becomes much elongated and the leaves shorter, broader, yellow, and brittle. When flowers are developed on these affected shoots, they are more or less abortive and sickly, and no fruits or fertile seeds arise therefrom. Frequently the shoots blossom prematurely. For example, we can at once detect by its elongated rosette-leaves when *Primula Clusiana* and *minima* are infected by *Uromyces Primulae integrifoliae*, and it may be observed when this is the case that the shoots do not wait until the next spring to develop the flowers laid down in the summer, as usual, but open them in the autumn of the same year instead.

The Cowberry (*Vaccinium Vitis-Idaea*) is especially worthy of notice among low woody plants, because two kinds of parasite attack its shoots. *Melampsora Goppertiana*, in the Teleutospore-stage, causes a marked, gouty thickening in the cortical parenchyma, which is converted into a spongy tissue; at first it is flesh-coloured, but soon assumes a chestnut-brown tint. The stems elongate very much and grow vertically upwards; and when several of them close together are thus attacked they present a besom-like appearance. The foliage-leaves are much

farther apart than in the healthy plant on account of this stretching of the stem. The lower leaves of the shoot are transformed into small fringed scales, and the upper ones are so much shortened that their outline becomes almost circular. The second parasite to which the Cowberry shoot is subject is *Erobasidium Vaccinii* (a near ally of the already mentioned *Erobasidium Lauri*, p. 521). The stem becomes pale rose-red colour, and rather thickened and spongy, but it does not elongate much more than usual; the leaves become blistered and curiously convex on the



Fig. 359.—A Witches' Broom on the Silver Fir, produced by *Aeidium elatinum*.

under surface. The substance of the infected leaves becomes brittle and loses its chlorophyll. A red tint appears in place of the green, especially on the upper surface of the leaf, whilst the lower surface, on which the spores develop, looks as if it had been dusted over with flour. Usually the buds develop prematurely on these shoots, *i.e.* the buds which, under ordinary circumstances, would not develop until the next year push out and form new shoots shortly after they have been laid down. The axes of these shoots, however, remain short; their leaves are closely crowded, red in colour, and sessile. From a distance the premature shoots look like large double red flowers inserted in the dark green of the non-infected Cowberry bush. The shoots which develop prematurely on the shrubs of the Bog Whortleberry (*Vaccinium uliginosum*) by the action of *Exobasidium Vaccinii* are often met with in alpine regions, and are even more noticeable on account of their fiery-red

colour. The Bearberry (*Arctostaphylos Uva-ursi*), *Ledum palustre*, and the Marsh Andromeda (*Andromeda polifolia*) are subject to similar metamorphoses at the hands of *Exobasidium Vaccinii*, so that *Vaccinium Vitis-Idea* may be regarded as typical of them.

When the shoots of the larger shrubs or trees are metamorphosed by parasitic Fungi attacking their branches, we have the formation of the structures popularly termed Witches' brooms, which were mentioned at the beginning of this chapter. The stimulus necessary for their formation is afforded in different plants by different parasites: on Barberry bushes (*Berberis vulgaris*) by *Æcidium Magel-hænicum* (to be distinguished from the common *Æ. berberidis*), on the Gray Alder (*Alnus incana*) by *Exoascus epiphyllus*, on the Hornbeam (*Carpinus Betulus*) by *Exoascus Carpinii*, on the Bullace (*Prunus insititia*) by *Exoascus insititiæ*, on other species of the genus *Prunus* by *Exoascus Cerasi*, on the Birch (*Betula verrucosa*) by *Exoascus turgidus*, on the Weymouth Pine (*Pinus Strobus*) by *Peridermium Strobi*, and on the Silver Fir (*Abies pectinata*) by *Æcidium elatinum*. Witches' brooms also occur on the Mastic tree (*Pistacia Lentiscus*), and on Beeches, Pines, Larches, Spruce Firs, &c., although hitherto we have not been able to ascertain definitely what parasitic Fungi are the cause in these cases. The Witches' broom of the Silver Fir has been selected and figured (see fig. 359) as a type of these peculiar structures. It always grows on one of the horizontally projecting lateral branches of the Fir, and raises its erect or curved twigs from the upper side, resembling, as it were, an epiphyte growing on the bark of the horizontal bough. The twigs are grouped in whorls and not in two rows, as usually happens in the lateral shoots of the Silver Fir. They are all shortened and thickened, and remarkably soft and pliable, because the cortical parenchyma has become spongy and the wood is only slightly developed. The buds, which in healthy tissue are egg-shaped, are almost spherical here. As in other instances of hypertrophied plant-members, we have a precocious development, a so-called "prolepsis", in these Witches' brooms. The buds swell earlier and unfold earlier than those of healthy twigs. The leaves remain short, yellow, somewhat crumpled, and fall off when a year old, while those of normal twigs are long, linear, straight, dark green on the upper side, and remain in position from 6-8 years. The growth of the twig is restricted; it dies off in a few years, and then, inserted on the dark green branches of the Silver Fir, remain the dry, bristling brooms, whose appearance has stimulated the imagination of the peasantry and given rise to the superstitions alluded to at the beginning of this chapter.

ALTERATION OF FORM BY GALL-PRODUCING INSECTS.

Certain members of the Arachnoidea, Diptera, and Hymenoptera, which attack and penetrate the tissues of living plants and incite the formation of peculiar excrescences, are known as gall-mites, gall-gnats, and gall-wasps. The

growths, like small rosy-cheeked apples, which occur on the foliage of Oaks, popularly known as "oak-apples", are amongst the best known. The terms "gall" and "gall-apple" were used by writers in the sixteenth century, and (like the Old English word *galle*, the French *galle*, and the Italian *galla*) are derived from the Latin word *galla*, used for these outgrowths by Pliny in his Natural History. The sixteenth-century writers distinguish between "gall-nuts" and "gall-apples", meaning by the former the small hard outgrowths on the leaves of Beech-trees. Afterwards the word *gall* was used for all the outgrowths produced by animals on green living plants. More than that—the hypertrophies described in the preceding chapter, produced in green host-plants by the various families of Fungi, are also included under the term. It has been proposed recently to substitute the word *cecidium* for *gall*, and to distinguish the excrescences as myco-*cecidia*, nemato-*cecidia*, phyto-*cecidia*, diptero-*cecidia*, &c., according as they owe their origin to Fungi, Thread-worms (Nematodes), Gall-mites (*Phytoptus*), Gnats (*Diptera*), &c. A systematic classification of this sort, on the lines of the classification of animals, might be of use to Zoologists, but to the Botanist its value is only secondary. He must, as in other similar cases, keep to morphology as the primary ground of classification, and has to arrange the structures according to their agreement in development. Moreover, in a general review, it is necessary to consider whether a whole group of plant-organs or one alone undergoes metamorphosis; and the starting-point of the outgrowth must also be ascertained; *i.e.* whether it is the foliage-leaves, floral-leaves, stems, or root-structures, &c., which are the head-quarters of the excrescence.

When the gall originating as the nest or temporary habitation of a single animal or colony of animals is limited to a single plant organ it is said to be *simple*; if, on the other hand, several plant organs are concerned in its production it is said to be *compound*.

Simple galls may, for convenience of description, be divided into (1) *Felt-galls*, (2) *Mantle-galls*, and (3) *Solid galls*. The Felt-galls are chiefly due to hypertrophied epidermal cells growing out into hairy coverings of various sorts and shapes; Mantle and Solid galls, however, are rather more complicated. In both cases insects are present in swellings of various descriptions, but there is this essential distinction:—The Mantle-gall is a hollow structure which, though it may arise in various ways and assume a multiplicity of forms, always has a portion of the surface of the affected organ for its lining—in other words, it is a chamber formed by hypertrophied growth *around* the place occupied by the insect. In the Solid gall, on the other hand, some spot is *pierced* by an insect and the eggs deposited *in* the tissues (not on the surface), the punctured spot forms a swelling with the larva inside, but the lining of the chamber is in no sense a portion or development of the original surface of the organ affected. Again, whilst in most mantle-galls the cavity of the gall is in open communication with the outside, and the insect can escape by this aperture (though this is not invariably the case), in the solid gall there is not such opening, and the insect

has to bore its way out. Needless to say, of both these types there are numerous modifications, but they fall into the two classes (of mantle and solid galls) according to their mode of development.

The majority of *felt-galls* are produced by gall-mites. They form cottony or felted growths on limited and sharply defined areas of green leaves and stems, the surface of which is otherwise smooth, or possesses but few hairs. Sometimes they have the form of small tufts, bands, or stripes, sometimes of large spots with irregular contour. In most instances the felt is situated on the under side of the foliage-leaf, and the gall-mite usually prefers the projecting veins to the green surface. In the Lime, Alder, Hornbeam, and Horse-Chestnut, the mites usually establish themselves in the angles formed by the lateral strands where they arise from the midrib, the projecting veins forming the framework for the felted hairs. In the Bramble (*Rubus*) and the Burnet (*Poterium*) it sometimes happens that the felt is continued down from the lamina to the leaf-stalk, and occasionally the green cortex of the succulent twig is covered with felted bands and spots. In some Brambles and Cinquefoils the sepals become furred by the action of gall-mites, the usual consequence being that the outline also becomes distorted. A swelling or slight hollowing of the green leaf-tissue very frequently accompanies the formation of felted galls, in which case the hairy covering is only visible on the concave side whilst the other remains smooth. This is most remarkable in the foliage of the Avens (*Geum*), Vine (*Vitis*), and Walnut-tree (*Juglans*), where a dozen white or brown-felted pit-like depressions are sometimes to be seen on the under side of a single leaf. The colour of the felted hairs is white in the leaves of Beeches, Limes, Bird Cherry, Brambles, Cinquefoils and Burnets, green in the common Maple, yellow in the Spindle-tree (*Euonymus verrucosus*), sulphur-yellow in *Alnus orientalis* and Black Poplar (*Populus nigra*), carmine red at first and then violet in *Alnus viridis* and in the Birches (*Betula alba*, *carpatica*, &c.), and brown in the Avens (*Geum macrophyllum*), Horse-Chestnut (*Æsculus Hippocastanum*), and in the Aspen (*Populus tremula*). The felted galls which are light in their young stages usually take on a brown tint afterwards. Microscopic investigation has shown that in the formation of felted galls, the epidermal cells, originally tabular in shape and closely fitting, swell out and become transformed into bent and twisted tubes generally shaped like a club or retort, the stimulus being afforded by a minute gall-mite (*Phytoptus*). These cells look like short hairs to the naked eye, and as they stand side by side in large numbers the covering has a velvety or felted appearance. The mites which produce the felt, deposit their eggs in the juicy hair-shaped cells, and their young live on the materials contained in them. It should be mentioned that formerly these velvety and felted coverings were regarded as Fungi, and were described as distinct genera under the names *Erineum* and *Phyllerium* (e.g. the gall known as *Erineum quercinum* on the leaves of *Quercus Cerris*). To this group belongs also the gall occurring on the Wood Meadow Grass (*Poa nemoralis*) consisting of cells which resemble root-hairs, which is produced by the gnat *Hormo-*

myia *Poa*. The hair-shaped cells are epidermal, and spring from the stem above the nodes: they break through the leaf-sheath which proceeds from the adjacent node, and are arranged in two groups, which grow in opposite directions, so as to wrap round the stem from the two sides. The whole hairy mass looks as if it had been parted into two. At first the hairs are white; later they become light brown, and when the gall is fully developed they have the form of brown felted strands, wound round the stems and firmly inclosing the larva of the gnat in question.

A large number of simple galls are grouped together under the name of *Mantle-galls*. The insects which give rise to them spend their lives on the surface of the leaves, where they multiply and attach their eggs to the epidermis. A growth is excited in certain layers of the cell-tissue by the stimulus which the animals exercise on their place of settlement. Cavities are thus formed which serve as dwellings for the animals and their brood, and which surround them like a protecting mantle. Mantle-galls may be divided according to their structure into *scroll*-, *pocket*-, and *covering-galls*. *Scroll-galls* are caused by gall-mites, leaf-lice, tree-hoppers, and flies, and usually occur on the blades, rarely on the petioles of the leaves. The surface inhabited by these animals, which, in the ordinary course of things would have spread out flatly, grows more luxuriantly on one side than on the other, and the result is the formation of a scroll, *i.e.* of a chamber in which the animals are hidden. It is always the side on which the animals live which becomes concave, and the leaf is usually curled up lengthwise. In the Alpine Rose (*Rhododendron*), Crane's-bill (*Geranium sanguineum*), and Orache (*Atriplex hastata*, *oblongifolia*, &c.), it is the upper side of the leaf which is tenanted by the insects, and is therefore the one to roll up; it is the lower side, however, in the Buckthorn (*Rhamnus cathartica*) and the non-climbing species of Honeysuckle (*Lonicera alpigena*, &c.). In many instances the whole leaf-lamina is rolled up, but more frequently the alteration is restricted to the edge of the leaf when the margin appears to be bordered with a swollen hollow cushion often corrugated or undulating. In the Alpine Rose (*Rhododendron ferrugineum* and *hirsutum*) both halves of the leaf-blade are rolled round (see figs. 360² and 360³), but usually the rolling is so slight that the gall has the form of a boat or hollow trough. Sometimes an alteration in the shape of the leaf accompanies the rolling. For example, the foliage of the Abele (*Populus alba*) on which *Pachypappa vesicalis* establishes itself when the leaves are very young, exhibits in addition to the rolling a deep hollowing of the blade. Instead of the short blunt lobes, long pointed segments are formed, which stand side by side when they are rolled up, and cross over one another in many ways so that the mantle-gall on the hollow side is shut in by a veritable lattice-work. The parts of the tissue brought into contact by the rolling do not fuse together, and therefore the cavity in which the gall-producing insects live is always in open communication with the exterior. In most cases the tissues concerned are thickened, brittle, more or less devoid of chlorophyll, and yellow in colour. Not infrequently a red pigment is formed in them, so that the outside of the gall has a yellowish-red colour. The scroll-gall produced by the hemipterous

Trioza Rhamni on the margin of Buckthorn (*Rhamnus cathartica*) leaves is very hard and thickened like cartilage. In many plants the epidermal cells lining the gall elongate into hairy structures, as in the felt-galls previously described. Their juicy contents are used as food by the young gall-mites. This is the case, for example, in the Alpine Rose (*Rhododendron ferrugineum*, cf. fig. 360³). Pocket-galls are closely allied to the scroll-like forms. The tissue of the leaf-lamina or



FIG. 360.—Galls.

¹ Covering-galls on the petiole of the Black Poplar (*Populus nigra*) produced by *Pemphigus spirotheca*. ² Scroll-galls on the leaves of an Alpine Rose (*Rhododendron ferrugineum*) produced by gall-mites. ³ Transverse section of one of these galls. ⁴ and ⁵ Bud-galls on the branchlets of the Wild Thyme (*Thymus Serpyllum*) produced by gall-mites. ⁶ Blister-like galls on the leaf of the Red Currant (*Ribes rubrum*) produced by *Myzus ribis*. ⁷ Part of the leaf seen from below. ⁸ Vertical section of a portion of this gall. ⁹ Solid gall on the leaf of the Gray Willow (*Salix incana*) produced by *Nematus pedunculi*. ¹⁰ The same gall cut open. ¹¹ Part of the wall of this gall in vertical section. ¹², ¹³, ¹⁴, and ¹⁵ natural size; ⁵ and ⁶ $\times 4$; ⁸ and ⁷ $\times 8$; ⁸ and ¹¹ $\times 50$.

petiole and sometimes that of the cortex in young twigs is subjected to a stimulus where the animals (gall-mites, leaf-lice, diptera) settle, with the result that a hollow protuberance arises whose excavated cavity serves as a temporary dwelling for the insects. The protuberances exhibit a great variety of form and shape, and they differ considerably in their internal structure. The following are the most noticeable forms. First, the plaited galls. They form deep, plaited, sometimes twisted channels in the leaf-tissue which open on the upper side by a narrow hole, and

project like weals on the lower surface of the leaf. The growing tissue which forms the floor of the channel is yellow and often lined with short hairs. The channel usually follows the course of the larger veins of the lamina, and sometimes actually traverses one. Plaited galls are produced by gall-mites. The best known are those on the foliage of *Carpinus Betulus*, *Clematis Flammula* and *C. recta*, and *Ribes alpinum*. Wrinkled galls come next to the plaited form. The protuberance is here limited to the green tissue shut in by strong rib-like projecting veins, and is only shallow; the upper side of the leaf has bulgings and protuberances and the lower pits and cavities. The protuberances are always developed in numbers close together, so that the leaf looks very much wrinkled in that region. Examples of this form are furnished by the wrinkled galls on the Elm (*Ulmus campestris*; see fig. 361¹) produced by the leaf-louse *Schizoneura Ulmi*, and on the Red Currant (*Ribes rubrum*; see figs. 360^{6, 7, 8}) by another leaf-louse, *Myzus ribis*. In the latter several wrinkles are usually united into large blister-like protuberances, red on the outside, and covered with jointed cellular structures bearing glands which look to the naked eye like short hairs. This form, though resembling certain felted galls, is distinguished from them by the different form of the hairs arising in consequence of the stimulation. In the Mouse-ear Hawkweed (*Hieracium Pilosella*) leaf-lice (*Psyllodes*) produce minute protuberances with narrow mouths, which stand out from the lower side turned towards the ground like small warts, and when they occur close together give a corrugated appearance to the leaf. Hollow protuberances of this sort arising upon restricted areas of the leaf-surface, and growing very actively, give rise to bag or sack-like structures attached by a very narrow neck. From their resemblance to a head such galls are sometimes termed capitate galls (*Cephalonion*). In others, where the outgrowth is fairly thick-walled and in form horn-like, the designation horn gall (*Ceratonion*) has been given. Between these forms numerous intermediate forms exist which may be compared to pockets, bags, nails, &c. Many of these galls project from both the upper and lower side of the leaf, as though a nail had been driven through it—hence the last-mentioned name. The capitate-gall of the Sloe (*Prunus spinosa*), caused by a gall-mite, projects almost as much from the under as from the upper side, whilst the similar gall on the foliage of the Bird Cherry (*Prunus Padus*) rises on the upper side as a long pocket, but below only projects like a small wart. Many capitate and horn-like galls are developed only on one side, and here again there is a very great variety. When the protuberances are due to mites the cavity always opens on the lower side of the leaf. Both the inner wall and mouth of the cavity are covered with hairs, and sometimes the aperture seems to be actually plugged up by them. In the bag-shaped protuberances produced by the leaf-louse *Tetraneura Ulmi* on Elm leaves, a relatively large slit is formed just at the narrow part of the bag at the moment when the insects leave the cavity (see fig. 361⁵). The external surface of the protuberances caused by mites on the foliage of Alders (*Alnus*), Maples (*Acer*), and Limes (*Tilia*) is smooth, in those of the Bird Cherry (*Prunus Padus*),

and Wayfaring Tree (*Viburnum Lantana*) ciliated, whilst in the inflated galls of the Elm caused by the white woolly leaf-louse (*Schizoneura lanuginosa*), it is covered with fine hairs like velvet. The capitate galls on the foliage of Maples, Alders, and Limes, of the Guelder-rose and Strawberry, are scattered abundantly over the whole lamina; in the Sloe they stand out chiefly from the margin of the leaf, and in Elms they occur singly or in groups on its central portions. The size of these galls depends upon their distribution. Those which rise in hundreds from the



Fig. 361.—Galls.

1-3 Solid galls on a Rose-leaf; 1 of *Rhodites Rosa*, 2 of *Rhodites Eglanteria*, 3 of *Rhodites spinosissima*. 4 Wrinkled galls on an Elm-leaf (*Ulmus campestris*) produced by *Schizoneura Ulmi*. 5 Purse galls on the same leaf, produced by *Tetraneura Ulmi*. 6 Covering gall on the same leaf, produced by *Tetraneura alba*. 7 Solid galls on the leaf of the Purple Willow (*Salix purpurea*), produced by *Nematus gallarum*. 8 Solid galls on the leaves of the same Willow, produced by *Nematus resicator*.

same lamina have a diameter of 1-3 mm., while those which occur singly or in small groups, often attain a diameter of 2-3 cm.

Contrasting with these embossed or *pocket-galls* are the *covering galls*, forming a third type of mantle-gall. In these, as in the embossed forms, the insects producing the galls live in their cavities, but the course of development is quite different in the two cases. The tissue round the place where an animal has settled or where an egg has been fastened to the epidermis in this type begins to grow, rising up in the form of a fleshy mound or wall which continues to grow until the animal is wholly roofed in. The cavity in this case does not arise from an excavation (as in the embossed or "pocket" type), but from an overarching of the tissue. The

external appearance of these galls is very varied. One of the simplest forms occurs on the leaves of the Ash (*Fraxinus excelsior*, see fig. 362³), where it is produced by the gall-gnat *Diplosis botularia*. The insect having laid its eggs in the channelled depressions above the leaf-veins, fleshy cushions arise on either side of the groove which meet above and roof them over. The cushions of tissue forming the roof do not fuse; their succulent edges merely meet, and when the time comes for the gall-gnats to leave their temporary abode the tissue dries up and shrivels,



Fig. 362.—Galls.

¹ Pine-apple gall on twigs of the Spruce Fir produced by the Spruce-gall Aphis (*Chermes abietis*). ² Covering gall on the petiole of the pyramidal Poplar (*Populus pyramidalis*) produced by *Pemphigus bursarius*. ³ Covering galls on an Ash leaf (*Fraxinus excelsior*) produced by *Diplosis botularia*. ⁴ Covering gall on Pistacia (*Pistacia Lentiscus*) produced by *Pemphigus cornicularius*. ⁵ Solid galls on the cortex of *Duvaua longifolia* produced by *Cecidoses Eremita*. ⁶ Longitudinal section of one of these galls. ⁷ Capsule galls on the leaf of the Turkey Oak (*Quercus Cerris*) produced by *Cecidomyia cerris*. ⁸ One of these galls cut through with the operculum still firmly attached, and ⁹ the same with the operculum falling away; $\times 3$. The remaining figures natural size.

leaving a gaping slit as shown in fig. 362³. The same thing happens on the leaves or rather leaf-veins of the Stinging-nettle (*Urtica dioica*) and of the Alder (*Alnus glutinosa*), where the galls are produced by gall-gnats (*Cecidomyia urticae*, *alni*), and on the midrib of Elm leaves (*Ulmus campestris*; see fig. 361⁶), where the galls are produced by a leaf-louse (*Tetraneura alba*).

The so-called turpentine gall-apples (*Carobe di Giude*; see fig. 362⁴), which

are caused by leaf-lice on various species of *Pistacia*, also belong to the covering class. The rudiment of a foliage-leaf, which in the normal course of events would have developed into a pinnate leaf with dark-green elliptical leaflets, grows out into a pod-like structure not unlike a locust-bean (fruit of *Ceratonia Siliqua*). These galls are longitudinally grooved, and it can be seen more or less distinctly that the furrows correspond to the edges of the leaflets, only here the leaflets have become wrapped in, very much thickened and elongated, and fused with one another. In the cavity inclosed by the fused leaflets lives a colony of leaf-lice (*Pemphigus cornicularius*) which have developed under the protection of the gall. When it is time for them to leave the cavity the top of the pod opens by the separation and bending back of the tips of the fused leaflets which form the wall of the cavity (see fig. 362⁴). The Chinese galls of commerce, produced also by Aphides (on *Rhus semialata*), develop much in the same way. They are hollow, irregularly pear-shaped structures with thin walls covered externally with a gray down. Two other covering galls which deserve special mention on account of their form arise on the petioles of the Poplar, particularly on the species *Populus nigra*, *pyramidalis*, and *dilatata*. The one, caused by a leaf-louse, *Pemphigus hirsarius* (see fig. 362²), consists of a smooth expansion, red in colour externally, on the upper side of the grooved petiole. If the local swelling be cut through it is seen to be hollow, the cavity in which the leaf-lice live being shut in by thick fleshy walls. The fleshy tissue of the walls is formed by a growth of the cells round the place where the gall-producing insect has settled. A hole is formed at a point remote from the petiole (where the growing tissue met and formed a dome) as soon as the time comes for the inhabitants to make their exit. This is bordered by thick lips as shown in fig. 362². The other gall which appears on Poplar petioles, produced by *Pemphigus spirotheca*, is formed by the thickening of the edges of the grooved petiole, which rise up as fleshy cushions and meet above the depression. At the same time the petiole undergoes a spiral twisting, and a gall is thus produced whose cavity is spirally twisted like the interior of a snail's shell. The thickened edges of the petiole do not fuse; at first they fit close to one another, but later on they separate, and a spiral hole out of which the white, downy leaf-louse can creep is the result (see fig. 360¹, p. 531).

We will now leave the mantle-galls and pass on to a consideration of the *solid* or *tubercular galls*. These are of the nature of swellings of limited size on single plant-organs, and are produced by insects which *pierce the plant-tissue and lay their eggs in the wound*. In this way either the epidermis of the chosen spot alone is injured, or the egg is inserted into the deeper-lying tissues. In both cases an active cell-division is incited in the neighbourhood of the injury. If, however, the egg has only been deposited in the epidermis, the larva which arises from it must penetrate into the interior of the now swollen tissue: when the egg is laid at once deep down this farther penetration on the part of the larva is of course unnecessary. The cavity in which the larvæ dwell may be called the larval chamber, and this sort of gall can be classified according to the number of chambers which it contains,

whether only one or several (*cf.* figs. 363² and 363⁷). A great variety is met with in the structure of the wall of the larval chamber. It always has a layer of juicy, thin-walled cells immediately surrounding the egg, known as the medulla or pith of the gall, and an outer layer which surrounds the inner like a skin or bark (see fig. 360¹⁰). In most instances a third layer is inserted between them which consists of very hard cells forming a protective layer. It should also be noted that the layers of the wall of the gall separate in many instances, so that it is possible to distinguish an "inner" and an "outer gall". The gall-pith furnishes the larva with food when it emerges from the egg, and for this purpose the cells are stored with nourishing substances. The development of the pith takes place with great rapidity, and begins as soon as the egg has been laid in the tissue. The larva when hatched finds the inner wall of the chamber which has been fitted for its temporary abode always provided with the necessary food, and it immediately attacks and devours the juicy tissue with great avidity. The cells which are demolished, wonderful to relate, are replaced almost at once. The cells of the gall-pith remain capable of division as long as the larva in the chamber requires food, and the surface cells which have been devoured in the gall-chamber are soon replaced by new cells from below, just as grass which has been mown down or cropped by cattle in a meadow sends up new stems and leaves. The spheroidal gall arising on the leaves of *Salix incana* (*cf.* fig. 360⁹) has only one chamber, and here the larva lives at the expense of the starch and other food-materials contained in the extremely thin-walled cells which constitute the gall-pith (fig. 360¹¹). The larva traverses the chamber in a circle, beginning the destruction of the cells at a certain place and eating on as it continues its peregrination (fig. 360¹⁰). New cells have already been formed for its nourishment by the time it again reaches the place from which it started.

The hard and cortical layers are modified in very many ways as protective measures against the drying up of the gall in summer on the one hand, and against the attacks of birds and larger animals on the other. For the latter purpose the cortical layer is often fashioned like the pericarps of fruits which have to protect the seeds (*cf.* p. 442). This also explains the bitter substances, hard skin, furry coat, bristling processes, and numerous other protective structures which are developed in and on galls just as on pericarps, and which contribute not a little to the remarkable similarity between galls and fruits. Many peculiar developments on the surface of these fruit-like galls cannot indeed be explained in this way, but, as in so many other cases, we conclude that they must afford some other advantage concerning which our understanding is still at fault.

The external similarity between fruits and solid galls affords us useful points for classifying the latter into groups, which we may name berry-like, plum-like, apple-like, nut-like, capsule-like, &c. The currant gall produced by *Spathogaster baccarum* on the male catkins of the Oak has not only the form and size of a Red Currant berry, but is also succulent and coloured red, and when several of these galls are formed on the same inflorescence it looks at first sight just as if racemes

of red currants had been borne by some chance or other on Oak twigs. The galls produced by the Beech-gall gnat (*Harmomyia fagi*) on the foliage of the Beech resemble small plums, being surrounded by a hard layer which consists of a stone kernel and a layer of cells which might be compared to the fleshy part of a plum. The galls caused by gall-wasps of the genus *Aulax* on the nutlets of many Labiatae, especially on *Nepeta Pannonica* and *Salvia officinalis* also assume the form of stone-fruits. The insect lays its eggs in one of the four nutlets developed at the base of each flower; and within a week this grows into a smooth greenish-yellow ball which has the external appearance of an unripe cherry. A section through it shows that it possesses also the same structure as a cherry, plum, or stone-fruit in general. The succulent outer layer surrounds a hard stony kernel, but in the cavity of the kernel there lies the white larva of the gall-producer instead of the seed. These galls fall off just like fruits in July, and lie on the ground during the winter; and the mature insect does not bite an opening in the wall of the gall through which it can emerge until the following year. It has been already remarked at the beginning of this section how strong is the resemblance between apple-fruits and the spherical oak-galls, known as oak-apples, which are produced by various Cynipedes (see fig. 364³), together with the small red-cheeked galls produced by *Rhodites Eglanteriae* and *Nematus gallarum* (see figs. 361² and 361⁷) on Rose and Willow leaves respectively. Pith-galls which resemble certain dry fruits are very common. Those produced on the green cortex of young Oak twigs by *Aphilothrix Sieboldi* (see fig. 364¹) remind one of the fruits of species of *Metrosideros*, those produced by *Neuroterus lanuginosus* and *Spathegaster tricolor* on the leaves of the Turkey Oak (*Quercus Cerris*; see figs. 364¹¹ and 364¹⁴) have a decided similarity to the indehiscant fruits of the Wood-ruff and of the Goose-grass (*Asperula odorata* and *Galium Aparine*). The "spangle" galls produced on Oak-leaves by the gall-wasps *Neuroterus fumipennis* and *numismatis* resemble the fruits of *Omphalodes* (see figs. 364¹² and 364¹³), and the galls on the leaves of *Durania longifolia* produced by an insect *Cecidioses Eremita* have the form of a capsule which opens by an operculum (see figs. 362⁵ and 362⁶). Like fruits these galls may appear in all imaginable conditions with smooth, warted, or rugged surfaces, or covered with woolly or velvety hairs, with bristles or spines, fringes or claws, or even with moss-like outgrowths. The galls with moss-like covering occurring on the Wild Rose have been known from remote times as Bedeguars. They are caused by the Rose-gall wasp (*Rhodites Rosae*), which deposits its pointed, sometimes hooked eggs early in the spring in the substance of an undeveloped leaf while it is still folded up in the bud. The growth of the leaf becomes altered, the first sign being the development of numerous hairs. The larvæ, when they creep out of the eggs, penetrate deeper into the tissue of the leaf, and it swells out into a solid gall containing as many chambers as there are larvæ. Hairs and fringes continue to form on the exterior till those curious structures are formed which were said to have the power of inducing a peaceful sleep when laid under the pillow. Usually the stalks of the

young bud-leaves are pierced and then the upper portion of the leaf becomes atrophied. More rarely is the egg laid in the epidermis of one of the leaflets, in which case the leaves attain their normal size and only this particular leaflet is decorated with little bedeguars, as shown in fig. 361¹. When the petioles of three young leaf-rudiments are pierced simultaneously, as often happens, three single galls are produced close together on a shortened axis, and the whole structure may then attain the size of a pine-cone.

The portion of meristematic tissue which is pierced by the insect when it deposits its eggs sometimes remains an open passage; but more often a corky tissue is formed at the wounded spot which quite closes the chamber wherein the larva dwells. Under these circumstances the insect when it emerges must itself make an exit-passage from the gall, and this it does by biting a hole through it with its mandibles (see fig. 364³). The gall-wasps (Cynipedes) invariably leave the chamber which has hitherto served them both as a safe habitation and as an inexhaustible storehouse in this way. This does not occur, however, in some of those solid galls which owe their origin to gall-gnats of the genera *Hormomyia*, *Diplosis*, and *Cecidomyia*, for example, in those on the leaf-blade and petiole of the Aspen (*Populus tremula*) produced by *Diplosis tremulae* and on the leaves of Willows (*Salix Caprea*, *cinerea*, *grandifolia*) by *Hormomyia Capreae*. Here the exit-passage is formed during the development of the pith. The gall consists, as in most other solid galls, of a pith, a hard layer, and an epidermis, but the enormously developed pith and the hard layer do not quite entirely surround the small larval chamber, they leave a small aperture on the part of the gall which is most arched. As long as the epidermis stretches over this place the mouth of the passage is of course not evident, but when the time comes for the insect to quit the chamber a gaping slit is spontaneously formed in the tense epidermis. In many instances the insect or the pupa as it pushes forward may break through the thin skin. A peculiar closure which might be compared to a lid is formed in the common solid galls which are produced so abundantly on Beech leaves by *Hormomyia fagi* and which have been already alluded to. Just as the pupa of many Lepidoptera projects out of the hole in the cocoon which the caterpillar has spun for it far enough to allow the insect to fly away uninjured when it emerges, so that of *Hormomyia fagi* presses through the lid-like closure at the base of the gall, and the winged insect comes out leaving the chrysalis-case behind it.

The opening of some solid galls, which resemble operculate capsules, and which may be termed capsule-galls, is especially remarkable and requires a more detailed description. As long as the larva or grub can remain and obtain food in the larval chamber the gall is completely closed, but when the time approaches for it to move its quarters and to enter the pupal stage in the ground a circular line of separation is formed in the tissue, and the part of the wall within the circle comes away as a lid. The process is seen very prettily in the gall produced on the leaves of the Turkey Oak (*Quercus Cerris*) by the gall-gnat *Cecidomyia cerris* (see fig. 362⁷). In its closed condition the gall is a firm rounded chamber

so embedded in the leaf that it projects on the upper side as a small pointed cone, and on the lower side as a disc covered with a thick coating of hairs. In the autumn a circular piece like a lid becomes detached from the lower side of the chamber. It corresponds exactly with the extent of the hairy disc, and is so sharply defined that it looks as if it had been cut out with a knife (see figs. 362⁸ and 362⁹). The operculum falls off, and the larva which had emerged from the egg and which has lived all the summer in the gall-chamber tumbles out and makes its way into the ground, where it begins to spin. By the next spring it has entered the pupal stage, and the gall-gnat creeps out of the chrysalis about May.

Still more peculiar are the galls produced by *Cecidoses Eremita* on the green

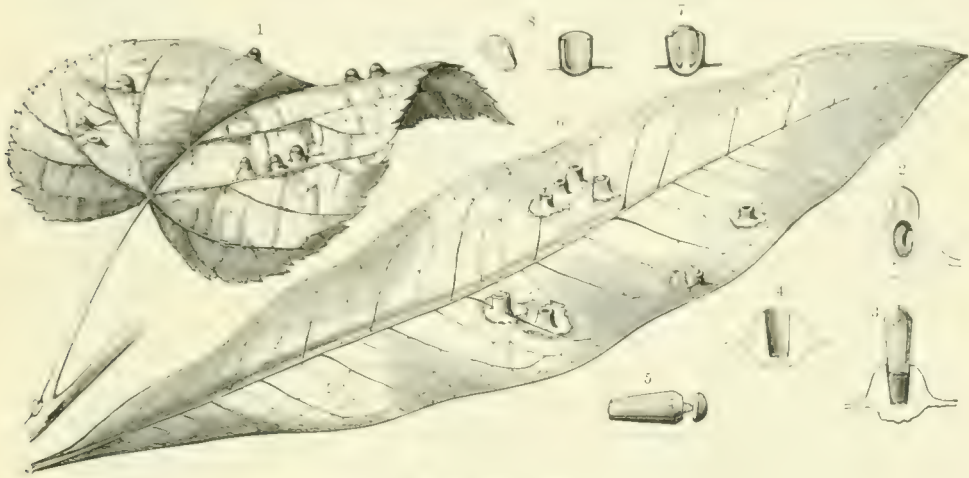


Fig. 363.—Solid Galls.

- ¹ Capsule-like galls on a leaf of the Broad-leaved Lime (*Tilia grandifolia*) produced by *Hormomyia Réaumuriana*. ² Longitudinal section through one of the galls, showing the maggot in the interior; $\times 2$. ³ Longitudinal section through a capsule gall from which the inner gall is just being extruded; $\times 2$. ⁴ Outer gall after the extrusion of the inner gall; $\times 2$. ⁵ Inner gall at the moment when the operculum is thrown off; $\times 2$. ⁶ Capsule-galls on the leaf of a Brazilian species of *Celastrus*. ⁷ Longitudinal section through one of these galls; $\times 2$. ⁸ The same after the inner gall has fallen out; $\times 2$. ¹ and ⁶ natural size.

cortical tissue of young twigs of *Duraoia longifolia*, a South American representative of the Anacardiaceæ (see figs. 362⁵ and 362⁶). The gall is quite spherical and very hard, and its large cavity conceals the caterpillar which has been hatched from the egg. When the time draws near for the formation of the pupa, a plug with a projecting rim is developed on the side of the gall furthest from its point of attachment. When the plug is pushed out a circular hole is left which leads into the gall-chamber through which the caterpillar escapes from its dwelling. People who have not seen these galls with their own eyes might almost think this description was the work of imagination. And yet there are still more wonderful forms in this class of gall-structures. On the foliage of the Lime (*Tilia grandifolia*) a growth arises round the eggs of the gall-gnat *Hormomyia Réaumuriana* which at first has the form of a flat lens inserted in the green tissue of the blade, but which gradually enlarges until it projects from the upper side like a

blunt cone and from the lower as a hemispherical wart. The gall-chamber is inhabited by the maggot of the gall-gnat. The top of the conical part loses its colour in July and becomes yellow and brown, and a rim is formed around its summit. On cutting a vertical section through the gall at this stage it is seen that the tissue forming the wall of the chamber consists of two parts (see figs. 363²). The inner layer, which contains the maggot, is surrounded by an outer one which gradually passes into the green substance of the leaf and extends up to the rim just mentioned. The whole structure has separated into an "outer" and an "inner" gall, the inner gall resembling an egg lying in an egg-cup (*cf.* fig. 363²). During the summer the inner gall separates completely from the outer and is actually thrown off by it. For the accomplishment of this the tissue of the outer gall swells up very much, so that it exercises a pressure on the inner gall which is shaped not unlike a cone, somewhat narrower below than at the top (see fig. 363³). The extruded inner gall falls on the ground below the Lime-tree and assumes a dark-brown colour: the outer gall remains as a little crater embedded in the leaf-blade and ultimately shrivels up (*cf.* figs. 363¹ and 363⁴). The detached inner gall is smooth at the blunt and previously upper extremity, and striated at the other; it is not unlike a detached composite-fruit. The gall-gnat within feeds for a little time longer on the succulent lining, and then rests through the winter; in the spring it makes its escape. To do this it bites a ring-shaped groove below the conical top of the gall and presses against the roof, which, owing to the breaking of the tissues around the ring, comes away like a lid (see fig. 363⁵). A similar state of affairs prevails in a gall formed on the foliage of a Brazilian species of *Celastrus* (see figs. 363^{6, 7}), but here the inner gall (which comes away) has several chambers, and the outer gall has the form of a cup set in the green blade.

The place of origin of all these solid galls depends of course upon the insects producing them. These are usually very fastidious about the place where they will lay their eggs, and it is truly astonishing with what care they search out spots difficult of access, and at once favourably situated as regards food supply and likely to afford a safe habitation for their offspring during the larval stages. The small gall-wasp *Blastophaga grossorum* lays its eggs in the ovaries of the "gall-flowers" in the interior of the figs of *Ficus Carica* (see p. 160 and figs. 240¹⁴ and 240¹⁵, p. 157). The gall-wasps *Andricus amenti* and *Neuroterus Schlechtendali* deposit them in the stamens of the Turkey Oak; the gall-wasp *Cynips caput-medusæ* lays hers in the side of the bract-scales which surround the pistillate flowers of the Oak (*Quercus sessiliflora* and *pubescens*), and so produces a gall with innumerable stiff-pointed fringes entangled with one another which ward off the attacks of other animals (see fig. 364¹⁰). Countless gall-producing insects deposit their eggs on the lower side of foliage leaves, some preferring the lamina, others the veins. *Andricus curvator* prefers the margin of Oak leaves, *Diplosis tremulæ* the petiole of the Aspen at its junction with the blade. Several gall-wasps, as, for example, *Andricus astivalis* and *Andricus grossulariar*, seek out the floral receptacle in the male catkins of the Turkey Oak for the deposition of their eggs, whilst

several Cynipides, e.g. *Aphilothrix Sieboldi* (see fig. 364¹) lay their eggs in the green cortex of the young twigs. Solid galls are very rare on roots, but they do occur



Fig. 364.—Various Oak-galls.

- ¹ Solid galls on the cortex produced by *Aphilothrix Sieboldi*. ² Bud-gall from a foliage-bud produced by *Cynips Hartigii*. ³ Solid galls on an Oak twig produced by *Cynips Kollar*. ⁴ One of these galls cut in half. ⁵ Bud-galls from foliage-buds produced by *Cynips lucida*. ⁶ One of these galls cut in half. ⁷ Leafy bud-galls produced by *Aphilothrix gemmae*. ⁸ Bud-galls from foliage-buds produced by *Cynips polycera*. ⁹ Longitudinal section through one of these galls. ¹⁰ Gall on the pericarp of *Quercus pubescens* produced by *Cynips caput-medusae*. ¹¹⁻¹⁴ Spangle galls on a leaf of the Turkey Oak (*Quercus Cerris*); ¹¹ produced by *Neuroterus lanuginosus*; ¹² by *Neuroterus numismatis*; ¹³ by *Neuroterus fumipennis*; ¹⁴ by *Spathegaster tricolor*.

in this situation in the oak, being produced by the gall-wasps *Aphilothrix radialis* and *Biorhiza aptera*.

When several organs of a plant immediately adjacent to one another are concerned in the production of a gall it is said to be *compound*. Compound galls are for the most part produced from buds, and they are all comprehended under the general name of *Bud-galls*. They are extraordinarily varied in their characters, some being merely abbreviated axes clothed with scale-like leaves, in others only the base of the shoot is involved and above the gall it continues its growth quite normally, whilst in others again the axial portion of the structure is much swollen, and the leaves hardly represented at all. It is difficult to give any satisfactory classification of these bud-galls; still, for the sake of arranging our facts, we may distinguish these types, viz.:—the *ordinary bud-gall*, the *cuckoo-gall*, and *cluster-gall*. Ordinary bud-galls involve several, often all, the members of a shoot. The axis of the shoot is always deformed and abnormally thickened. The swollen portion contains in its interior one or several larval chambers surrounded by a pith-like layer. Two varieties of ordinary bud-gall may be distinguished. The first is leafless: no leaves are present, or, more correctly, they are transformed into tubercles, pegs, and knobs which merge insensibly into the swollen axis which contains the larval chamber. The second possesses leaves, the gall being covered with scale-like bracts or more or less fully developed green foliage-leaves. Amongst the leafless bud-galls the most interesting are those which are armed with special means of protection against the attacks of animals on the watch for the larvæ of the gall-wasps. The gall shown in figs. 364³ and 364⁴, produced by *Cynips polycera* on the leaf-buds of *Quercus pubescens* and *sessiliflora*, which to a certain extent affects a whole lateral shoot, has the form of a young Medlar fruit, and on it may be seen 3–5 metamorphosed leaf-structures projecting as stiff-pointed pegs which gradually pass into the tissue of the shoot axis. This gall is one-chambered, and the tissue of the wall has separated into an outer layer and an inner spherical pithy gall. The gall shown in fig. 364² is produced by the gall-wasp *Cynips Hartigii* which lays an egg in the middle of the leaf-bud of the Oak (*Quercus sessiliflora*). The bud does not develop into a leafy shoot, but into a small one-chambered gall with large tooth-like or club-like processes which represent metamorphosed leaves. The thickened angular ends of these projections fit closely to one another so as to form a sort of second outer coat to the gall-chamber through which hostile ichneumon-flies cannot penetrate. The gall much resembles the cone-fruit of a Cypress in the arrangement and form of its superficial processes. The galls produced from the buds of various Oaks (*Quercus pendulina*, *sessiliflora*, *pubescens*) by the gall-wasp *Cynips lucida* are still more peculiar (see figs. 364⁵ and 364⁶). They contain several larval chambers with abundant pithy tissue, whilst innumerable slender processes resembling lined twigs in being very sticky on the capitate thickened end project from their exterior. Ichneumon-flies and other animals hostile to the gall-producers take good care not to come into contact with these spikes which are to be regarded probably as transformed leaves springing from the swollen axis. Among the galls produced from leaf-buds belonging to this group there are some in which the leaves are merely indicated as tubercles. This is the case, for example, in the many-chambered,

spongy gall, red-cheeked on the sunny side but pale elsewhere, which is produced on the tips of the branches of the Oak by the gall-wasp *Dryoterus terminalis*, and looks very like a potato in shape. The leaves are only represented by small ill-defined knobs and ridges, just as in the potato. To this class of galls belongs also that to which the term "nut" is popularly applied, and even in commerce, the name has been transferred from this to the whole of the first group of compound galls (bud-galls). The "nut" is produced on the Oak by *Cynips calicis* as an angular and irregularly-grooved gall which originates at the end of a flower axis, and the cupule formed of several bract-scales as well as the ovaries are concerned in the growth. This class of galls also includes the irregular blunt swellings on Aspen twigs (*Populus tremula*), which are caused by the larva of a beetle (*Saperda populnea*), and in addition the many-chambered woody "canker cushions" as large as a nut which are produced on the branches of Willows by *Nematus medullaris*.

The gall shown in fig. 364⁷, which arises on various Oaks (*Quercus pedunculata*, *sessiliflora*, *pubescens*) by the action of the gall-wasp, *Aphilothrix gemma*, may be selected as a type of leafy bud-galls. It resembles the cone of a Hop or Larch, and is developed from a foliage-bud. It has a much-abbreviated swollen axis, whose tissue separates into an inner and outer gall, beset with numerous dry, brown lanceolate hairy scales having the form of bract-scales. Bud-galls which are covered with green foliage-leaves are produced by the gall-wasp *Andricus inflator* on the Oak, but they are more commonly met with on herbaceous plants, e.g. by *Urophora cardui* on *Cirsium arvense*, by *Diastrophus Scabiosae* on several Knapweeds (*Centaurea alpestris*, *C. Budensis*, *C. Scabiosa*), by *Aulax Hieracii* on various Hawkweeds (*Hieracium murorum*, *sylvaticum*, *tridentatum*, &c.). Usually the foliage-leaves are stunted, and not infrequently the blades of some of them are quite obliterated, so that the gall in that region is only furnished with scaly leaf-sheaths. A Sage growing in the Isle of Crete so often bears leafy bud-galls resembling a small Quince-apple, produced by a species of *Aulax*, that Linnaeus called it *Salvia pomifera*. The stem of this Sage is swollen out like a ball, and the spherical mass, covered with a gray felt of hairs on the exterior, is surmounted at the top with a group of small wrinkled leaves, which look like the persistent calyx of a Quince-apple. The best known and most widely distributed of these forms, found on the Hawkweeds named above, consist of knob-like swellings of the stem. The larval chamber is situated inside the enlarged pith, the ring of vascular bundles, which has undergone much shifting, forms the protective layer, and the cortex of the affected region of the stem forms the cortical layer of the gall. The epidermis is densely covered with hairs.

Leaving the galls which consist of modified foliage-buds, we pass on to such as consist of metamorphosed *flower-buds*. They arise from flower-buds in which small gall-gnats have laid their eggs. The larva hatched from the egg lives in the cavity of the ovary, or in one of its loculi when there are several, and this space, therefore, becomes the larval chamber. The corolla, which envelops the ovary in the flower-bud, remains closed, like a cap on the top of the larval chamber. The calyx becomes

inflated, enlarged, and sometimes fleshy. The whole gall resembles a bud or small bulb; it is not unlike one of those bulbils which so often arise instead of flowers on the flowering axis of certain species of *Allium*. They occur especially on the Bird's-foot Trefoil (*Lotus corniculatus*), where they are produced by the gall-gnat *Cecidomyia Loti*, on the various species of Mullein (*Verbascum Austriacum*, *nigrum*, *Lychnitis*, &c.) by *Cecidomyia Verbasei*, on several species of Germander (*Teucrium montanum*, *Scordium*, &c.), caused by *Lactomelopus Teucrii*, and on the Rampion (*Phyteuma orbiculare*), where they are produced by *Cecidomyia phyteumatis*.

Closely allied to these bud-galls are those remarkable gall-structures which are commonly known in Austria as "cuckoo-buds". The cuckoo is supposed to be concerned in their formation, just as it is in that of the frothy saliva-like masses deposited by the *Cicada* on the Cuckoo-flower (*Cardamine pratensis*). The name "cuckoo-galls" may be employed for the whole of this sub-group. They are characterized by their pale whitish colour, soft spongy tissue, and especially by the fact that they only involve the *base* of the shoot, while the upper end can continue its growth unaltered. In this respect they may be compared to a Pine-apple fruit, where the axis rises above the fleshy collective fruit (*cf.* p. 436) as a green leafy tuft, which does not lose its growing power even with the ripening of the fruit. The history of the development of cuckoo-galls is probably like that of covering galls; and the main distinction lies in the fact that in the former the gall is produced not merely from a *single* organ or some part of it, but from a *whole group* of adjoining plant-members. The best known and most widely distributed gall of this group is produced by the pine-apple aphid *Chermes abietis* on the twigs of the Spruce Fir (*Abies excelsa*, see fig. 362¹, p. 534). Early in the spring, before the foliage-leaves have begun to unfold, the parthenogenetic females, the foundresses of the colony, attach themselves each to the base of a young leaf and lay a mass of eggs at the spot to which they have adhered. The larvæ, hatching, penetrate the surrounding parts of the shoot with their beaks; the shoot swells, as do the bases of the needles, and a growth, the Spruce gall or Pine-apple gall results. The gall somewhat resembles a small Fir-cone about an inch long, with the surface divided into small convex areas, each bearing a short needle-like projection in the middle; these are the deformed needles, which, becoming swollen, touch each other on the outside of the gall. They are separate inside, so that the gall contains a series of cavities or chambers. In these chambers the larvæ live in numbers, either entering the chambers during the growth of the gall or being inclosed by the swelling of the surrounding needles—this point is not certainly determined. They remain in the small cavities so formed and feed, cast their skins, and multiply there. In August the gall begins to dry up, each of the small cavities opens by a slit in front of the green needle-point surmounting the cushion (see fig. 362¹, p. 534), and the winged insects now leave the place in which they have passed the spring and summer.

Cuckoo-galls are met with almost as frequently on *Stellatæ*, viz. on various species of Bedstraw (*Galium Austriacum*, *boreale*, *uliginosum*, &c.) and Woodruff

(*Asperula galioides*, *tinctoria*, &c.) as on Fir-trees. The infected parts of the shoot remain stunted, and white spongy cushion-shaped growths, which are somewhat grooved, arise at the bases of the leaves. Since the growing tissues of neighbouring leaves touch one another the grooves or channels form small cavities in which live the larvæ of the gall-producing gnats (*Cecidomyia Gailii* and *Asperula*). In the common Bedstraw (*Galium Mollugo*) these spongy growths arise, not from the bases of the leaves, but from the green cortex of the stem round the insertion of the leaves and lateral branches. They rise up as cushions and lobes, and several join together to form a sort of dome, under which the larvæ of the gall-gnat dwell. The foliage-leaves are scarcely altered in form, and when lateral twigs arise from the place they also are unchanged. It not infrequently happens that short lateral axes terminated by flowers spring up quite unmodified above the spongy white cuckoo-gall. Cuckoo-galls also occur on Cruciferæ, viz. on *Barbarea vulgaris*, *Nasturtium palustre*, *sylvestre*, and *Sisymbrium Sophia*. They are produced by *Cecidomyia Sisymbrii*, and originate principally at the bases of the flower-stalks half-way up the inflorescences. They look like spongy white bodies which surround the pedicels like the brim of a hat. As the growths from neighbouring pedicels meet together they roof over chambers which serve as habitations for the larvæ of the gall-gnats. Viewed from outside the galls appear like irregular white bodies inserted in the inflorescence, which remind one of the fruit of the white Mulberry-tree.

The term *cluster-gall* is reserved for that type of bud-gall in which the axis is much restricted or stunted and covered with densely crowded leaf-structures; it is in the chinks and recesses between the crowded leaves of these galls that the insects concerned pass the whole or a portion of their lives. The animals which cause the galls belong to very different classes. Gnats, leaf-fleas, leaf-lice, and mites are the commonest varieties. The gnats only live in the galls during the egg and larval stages, but the others pass their whole life there. They invariably settle on the end of a shoot while it is still undeveloped in the bud. The axis of the shoot remains more or less stunted in consequence of the influence the animals exercise on it and its leaves undergo fundamental alterations. The blade or sheath of the leaf is deepened and hollowed to afford sufficient space to the animals which have established themselves between them, and as these parts of the leaves touch one another recesses are formed not unlike those which are developed in fir-cones for the growing seeds. The sheathing part of the leaf is often rather thickened, and its succulent cells serve as food for the animals living in the gall; in other instances the hollowed leaf-blades are thickly covered with hairs, and this coat then has the same significance with regard to the insects as the felt of hairs on isolated leaves already described. Very different forms of galls are produced according as to whether the free ends of the leaves turn back or remain in contact, and whether the axis from which the leaves spring is more or less contracted. Sometimes they remind one of open rosettes, sometimes of closed balls, bunches and tufts, sometimes of pig-tails and witches' brooms.

Clustered galls may be divided into two classes, those which develop in the region of the *flowers* and those in the *'foliage* region respectively. The most noticeable and best known forms of the galls occurring in the foliage region on rudimentary leafy shoots are the following:—First, those peculiar structures on the tops of Willow twigs (*Salix aurita*, *Caprea*, *grandifolia*, &c.) which are popularly termed “Rose Willows”. They are caused by the gall-gnat *Cecidomyia rosaria*. The leaf-bud from which they arise keeps its axis quite short and develops on it numerous green leaves arranged like the petals of a double rose. The lowest leaves of the “rose” differ but slightly from the normal foliage of the particular species of Willow. Usually there seems to be only a shortening and broadening of the petiole and leaf-sheath, the green blade being almost unaltered. In the upper inner leaves, however, the sheath-like part of the leaf is much increased in size, and nearer the centre of the “rose” the leaves become scale-like. The leaf-blade has entirely disappeared, and the end of the contracted axis possesses only the remains of leaf-sheaths. It is worth noting that the number of leaves in a Rose Willow is always greater than would be found on an unaltered shoot of the same species. For example, if the number of leaves on the one-year-old shoot of the Sallow (*Salix Caprea*) is 25, the number in a “rose” on the same species would be at least twice as large. This can only be explained by supposing that a “prolepsis” has occurred, *i.e.* that not only the shoot laid down for the current year has developed, but also one originating from a bud of this shoot, which, under normal conditions, would not have developed until the following year. When autumn comes the rosette-shaped galls on the Willow bushes show up conspicuously at a distance because the leaves forming them do not fall off like the rest, but remain behind as brown dried structures at the ends of the branches. They are also found associated with the catkins. The rosette-shaped galls produced by the gall-gnat *Cecidomyia cratagi* at the tips of Hawthorn twigs (*Cratægus Oxyacantha* and *monogyna*) also claim attention. They are full of bristles and resemble tiny birds’ nests. The stimulus of the gnat larvæ excites a deeper and more frequent segmentation in the leaves and stipules. Narrower points and fringes which are much bent and which resemble the antlers of reindeers replace the broad lobes. Also soft spines with capitate ends rise up from the green cortex of the twigs and from the tissue of the leaf-blade, especially above the vascular bundles, and 3-5 of them often fuse together into cock’s-comb-like structures. These bristling rosettes on Hawthorn branches also remain long after the time the ordinary foliage falls off.

In marked contrast to the rosette-like cluster-galls are others whose leaves all fold together in a ball something like the leaves of a cabbage, the whole gall having a button-like appearance. The outer leaves are round and hollowed on their upper side, and they usually fold together like mussel-shells. The inner leaves have a similar form, but they are much smaller and more concave, and they have become succulent and paler in colour. The galls produced by *Cecidomyia genisticola* on *Genista tinctoria* and those which *Cecidomyia Veronicæ*

gives rise to on *Veronica chamædrys*, and which gall-mites produce on the Wild Thyme (*Thymus Serpyllam*; see figs. 360⁴ and 360⁵, p. 531), form white buttons on the ends of the shoots which show up conspicuously from the dark green of the surrounding foliage. The white colour is due to the fact that the outer leaves, which fold together like mussel-shells, are thickly covered on the outside with white hairs. *Cecidomyia Artemisia* produces on the branches of *Artemisia campestris* a closed cluster-gall which is cased in white wool like a shroud. On the other hand, the large, button-shaped, closed cluster-galls which are produced by *Cecidomyia rosaria* on Willows (*Salix purpurea*, &c.) and by a gall-mite on the spikes of the Brome-grass (*Bromus*) are green and smooth, or at least they have not more than the usual number of hairs.

On the shoots of the Yew (*Taxus baccata*), the Flax (*Linum usitatissimum*), *Euphorbia Cyparissias*, the Moss Campion (*Silene acaulis*), and several *Ericas* (*Erica arborea*, *carnea*, &c.) the influence of various gnats (*Cecidomyia Taxi*, *Euphorbia*, *Erica*, *scoparia*, &c.) produces galls with linear erect leaves crowded together into tufts. The base of the crowded leaves and the axis of the gall are usually rather thickened, so that it looks as if the linear leaves were set on a rounded button, and this is particularly marked in *Euphorbia Cyparissias*. This division includes the gall formations occurring on Juniper twigs (*Juniperus communis*), which are caused by the gall-gnat *Lasioptera juniperina*. The acicular leaves of the Juniper are arranged in whorls of three on normal shoots. By reason of the influence of the gall-gnat *Hormomyia juniperina* the whorls at the top of the twig become so changed that the last but one represents a cup bordered with three teeth in consequence of the broadening of the needles, while the terminal whorl is metamorphosed into a dwelling surrounded by three short leaflets. This gall closely resembles the cone of the Arbor Vitæ (*Thuja occidentalis*, *orientalis*, and *plicata*) in form.

An insect, *Livia Juncorum*, produces galls on various Rushes (*Juncus*), especially *Juncus alpinus* and *lamprocarpus*, which look like knots or tassels. The axis of the shoot is contracted, the sheathing portions of the leaves which cover one another are much widened, and the colour is pale except where it is reddened by exposure to the sun; their appearance is like the outer covering or top of a tassel. The stunted green blades which spring from the sheathing portions are thread-like and arranged as the loose strands of the tassel. Not infrequently short lateral shoots arise in the axils of some of the leaves, and then the whole structure looks like a bunch of tassels.

Closely allied to these cluster-galls on the stems of Rushes are such as resemble tufts and witches' brooms, produced by mites on the branches of hairy Willows, especially on the white Willow (*Salix alba*). Instead of the long leafy Willow rod which would have emerged under ordinary circumstances from a foliage-bud, a confused mass of twigs with short leaf-scales is developed which at first seems a perfect mystery. By careful examination it is seen that the axis of the shoot laid down in the bud has remained stunted, and that lateral

shoots have developed from the axils of its leaves. These lateral shoots again develop lateral axes in the axils of their leaves, and so on to the third, fourth, and fifth degree. Thus, in the course of a month, shoots have unfolded, which, except for the influence of the gall-mites, would not have followed one another for three, four, five, or even six years, and therefore these galls afford us another instance of what has been termed "prolepsis" or precocious development of structures which would not yet arise. Of course all the axes of these shoots are dwarfed and the leaves which clothe them are diminished in size. The shortening and diminishing increase gradually, so that the axes and leaves of the fourth and fifth degree are much smaller than those of the second and third. The last lateral shoots remain bud-like, and their small scaly leaves fold over one another like the bracts in the involucre of a Composite. The "witches' brooms" which are caused by gall-mites on Lilac (*Syringa vulgaris*) and Privet (*Ligustrum vulgare*) bushes are similar in nature to these closed galls on the Willows. Frequently the metamorphosis of the leaves on the axes of the third, fourth, and fifth degree includes those of the floral region, and such cases form to some extent a bond of union between cluster-galls on foliage and on floral regions, respectively.

One of the most remarkable changes exhibited by the gall-structures just mentioned, viz. the abbreviation of the axis, is of course not to be noted in cluster-galls in the floral region. The part of the axis which forms the floral receptacle does not grow into an elongated shoot, but always remains short, and the floral-leaves it bears stand close to one another, forming whorls in whose niches and recesses numerous small animals can hide. But these animals effect other very marked alterations by their stimulus. In some flowers, instead of the normal red, blue, white, or yellow petals, green leaflets appear which resemble foliage-leaves in character, and then we say that the flowers have become "green" or "leafy". In other plants the stamens are transformed into petals, and the flowers are said to be "double". Finally, it may happen that the carpels which are usually united together to form a syncarpous ovary stand on the receptacle as distinct structures, and that to a certain extent their union has been dissolved. In these cases we speak of "antholysis" (*cf.* p. 80). The influence of gall-mites also produces metamorphosed flowers which may be both green and double, and in which the pistil may have separated into its individual carpels.

The best flowers for observing these metamorphoses in all imaginable degrees are the small-flowered species of the Chickweed genus (*Cerastium macrocarpum*, *triviale*, &c.), several Caryophyllaceæ (*Lychnis Viscaria*, *Saponaria officinalis*, &c.), Cruciferae (*Cardamine uliginosa*, *Camelina sativa*, *Lepidium Draba*), Gentians (*Gentiana acaulis*, *rhetica*), Speedwells (*Veronica officinalis*, *saxatilis*) and Milfoils (*Achillea Millefolium*, *nana*). In Speedwells the petals come to resemble leaves. The bunches, rosettes, and balls of small green leaves replacing the flowers are set close together on the rachis of the inflorescence and form green racemes and tufts, sometimes even small witches' brooms. In *Veronica saxatilis* the rachis of the raceme, the pedicels, and the bracts are covered with hairs, which

is not the case when the plants are free from the mites; the foliage-leaves in the neighbourhood of the raceme are also lobed and deeply indented, which again is not the case in uninfected plants of this species. In the capitula of the above-named Milfoils the peripheral ray-florets as well as the central tubular ones become leaf-like, and this gives rise to the most peculiar forms. A capitulum is often separated into several stalked sub-capitula, the flowers being metamorphosed into green funnels with jagged mouths, and into small flat-lobed and toothed foliage-leaves, whilst short, green, scale-like leaflets rise from the midribs of these leaves representing the metamorphosed stamens. A very remarkable "doubling" produced by gall-gnats is to be observed in flowers of the Alpine Rose (*Rhododendron ferrugineum*). The stamens and carpels are changed into red petals by their influence. Since *Rhododendron* flowers have ten stamens and five carpels, there should be only fifteen red leaflets in the centre of each, but as a matter of fact there are double and treble as many, and there has been not merely a metamorphosis but also a multiplication of the leaves. The flowers of some plants which belong to the Valerians, especially of the Corn-salad (*Valerianella carinata*), of which a small umbellate cyme is shown in fig. 358², p. 523, are doubled by the influence of a gall-mite, but without any multiplication of the petals. The doubling is restricted to the transformation of the stamens into a whorl of petals. But we also have another peculiar alteration. The petals become enlarged to more than fifty times their normal size, and change into fleshy lobes which are fused with one another into a disc. As all these lobes bend back, and become concave below, cavities are formed under the flowers in which the gall-mites can dwell (see fig. 358³, p. 523).

The axis of the inflorescence and the stalks of single flowers are often thickened and fleshy in these cluster-galls, and they are also stunted and bent in the most varied manner. If several neighbouring pedicels fuse together, structures like cocks'-combs, or like a compressed and flattened branch, arise; to these the term *fasciation* is applied. Sometimes when numerous pedicels arranged in the form of umbels fuse together we have structures like coral-colonies, or irregular clumps which are beset with green flowers usually much reduced in size. This is the case in the fasciations of the Ash (*Fraxinus excelsior* and *Ornus*), which are caused by a gall-mite (*Phytoptus*), and which occur so abundantly that it looks as if the tops of the trees had been sown with them.

The enumeration, here, of various forms of galls commenced with the inconspicuous felt-galls on the under side of isolated foliage-leaves, and it ends with the complex cluster-gall, in which hundreds of flower-stalks and leaves are frequently concerned. Of course, only types of the individual groups which have been mentioned in this long series could be instanced, and we cannot make any attempt to describe all the gall-structures at present known, about 1600 in number. Whether the extension of gall-researches in tropical regions will yield new forms which stand outside the pale of the classification given it is difficult to say. Apparently this will not be the case. Perhaps thousands of hitherto unknown galls might be added

to the list, but we should expect that they would fall under one or other of the above-mentioned groups.

Gall-structures have a peculiar significance for the section of the *Natural History of Plants* which deals with the question of the origin of species, since they show most distinctly how fundamental deviations from the original plan of construction may occur in the adult condition of a portion of a plant.

We must be careful to remember always that the immense variety of structures which we call galls would not have existed except for the effect produced on the plants by mites, leaf-lice, gnats, wasps, &c. The foliage of *Rhododendron* would not have been rolled up, but quite flat, if gall-mites had not been present; the branches of *Pistacia Lentiscus* would have borne pinnate foliage with shining dark-green leaflets and not fleshy-red pods if they had not been attacked by leaf-lice; the leaf-bud of *Quercus pubescens* would have developed into a long leafy shoot instead of a body like a medlar if the gall-wasp *Cynips polycera* had not provoked the change; the foliage of *Veronica saxatilis* would not have been lobed like a hand, but would have had a slightly sinuous margin; and the upper leaves of *Thymus* would have been green, spoon-shaped, and smooth on the surface instead of circular and covered with white hairs, had no gall-mites settled on them. The flowers of *Rhododendron ferrugineum*, *Lychnis Viscaria*, *Veronica*, *Cardamine*, &c., would not have "doubled", and the stamens would not have changed into petals, if they had not been under the influence of gall-mites.

Of course, the influence of the animals can only produce these effects on parts of plants which are in an embryonic condition. Mature stems and leaves may be eaten and destroyed by insects, but they can no longer be metamorphosed. But the undifferentiated rudiments upon which the influence is effective are, so to speak, formless. Leaves, stems, and fruits arise from tissue-masses having the form of tubercles and cushions, and each tubercle or cushion originates from a few cells which give no indication of what is to develop from them. Nevertheless, experience teaches us that the plan of construction for the plant-member proceeding from these primitive forms is definitely laid down from the beginning for each species, and the idea that the plan of construction is rooted in the specific constitution of the protoplasm of the plant—*i.e.* in the cell or cells which form the primitive stage or rudiment of the developing leaf, stem, &c., is confirmed. If an alteration in this plan of construction is produced by these animals, it can only be by some alteration of the specific constitution of the protoplasm.

How the alteration is effected is just the puzzle which is at present occupying the attention of naturalists. Once it was thought that the formation of galls was the result of injuries caused in the growing tissue by the ovipositor or sucking organ of insects, but recent investigations have not confirmed this view. The cells actually injured by the insect in laying its eggs perish, and consequently lose the power of metamorphosis or of producing modified daughter-cells. Cork, closing over the wound, is always formed from the adjoining living tissue, but for a long

time no gall is produced. The eggs deposited in the tissue, or attached to it, are also incapable of directly inciting gall-formation. There is no marked alteration in the neighbourhood until the grub or larva leaves the egg and excretes a fluid substance. Then growing cells of the most varied description are formed adjacent to the larva, and these rapidly assume the peculiar forms which have just been described. This, of course, applies also to cases where the larva has been hatched from the egg at some distance from the spot and has had to seek out a tissue suitable for its dwelling, as also to instances where adult gall-mites and leaf-lice choose out a suitable place for the deposition of their eggs and then secrete a fluid round them when they lay them. If the animal dies, the growth and renewal of the tissue immediately ceases. The cells round the dead body turn brown and die, so that we may conclude the formation of the gall to be due solely to the substance excreted by living animals.

Those who investigate galls consider that it is chiefly the acrid "saliva" excreted by the larvæ to liquefy their food which acts on the cell-tissue of the dwelling they have selected, but there is no doubt that other excretions may also take part. The chemical composition of this substance is unknown, but we shall hardly be wrong if we include it in the group of nitrogenous compounds called enzymes which were discussed at vol. i. p. 464. Enzymes have the power of altering and decomposing substances, even through the cell-wall, and in this way we can account very simply for a whole series of otherwise inexplicable phenomena in the formation of galls. Moreover, urea or closely-allied nitrogenous compounds may be excreted, so that there is nothing to be said against the view that some of the substances diffuse into the interior of the plant-cells. It is at least certain that the fluid substances excreted by the gall-producing animals, in whatever way they influence the protoplasm in the plant-cells, do not kill it, but actually stimulate it to an extraordinary new activity directly demonstrated by the production of tissues with a definite external form.

Observation shows that these tissues are formed and fashioned differently from what they would have been without the influence of this substance. It follows, therefore, that the substances excreted by the animals have the capacity of affecting in some way the specific constitution of the protoplasm which determines the species in the plant-cells influenced by them. It is specially interesting to note in this connection that it not only is the protoplasm of the cells directly acted on by the excretion which is stimulated to an altered form of constructive activity, but that this stimulus is transmitted from cell to cell in ever-widening circles. The spruce-fir aphid *Chermes abietis* attaches itself firmly by its beak to the scale of a Fir bud, and can directly influence only a few cells of the young shoot hidden in the bud. Nevertheless thousands of cells on this shoot soon begin to assume an altered form, a proceeding which reminds us strongly of the action of a ferment (*cf.* vol. i. p. 505), and also brings to our mind the influence exerted by the spermatoplasm on the ovary. The spermatoplasm is only directly concerned with a few cells in the ovule, but these propagate the influence on all sides to

the carpels and to the receptacle, and sometimes even to the flower-stalk. All these parts would not have developed as they have done had it not been that the minute quantity of spermatoplasm of a pollen-grain had united with a minute cell in the ovule.

It will be convenient to consider here the already mentioned similarity between galls and fruits. If the leaf-rudiments in the bud of a *Pistacia* shrub are not affected by leaf-lice they develop into shining green pinnate foliage-leaves; but if the protoplasm in some of the cells has been altered by the excretions of *Pemphigus cornicularius* this same rudiment will assume the form of a carpel, and become fashioned into a hollow body deceptively like a pod. The fact that the *Pistacia* shrub bears plum-fruits and not pods makes it still more remarkable, for the structure arising from the effect of the animal's excretion, when mature, is not like the fruit of the *Pistacia*, as we should naturally have expected, but like that of a completely different plant species, viz. the Carob (*Ceratonia Siliqua*). The same is true of the metamorphosis caused by the excretion of a gall-gnat (*Lasioptera juniperina*) on the uppermost leaves of the Juniper (*Juniperus communis*) which assume a form very like the fruit of the Arbor Vitæ (*Thuja*), and many other instances might be mentioned in which galls are produced in certain species of plants by animal excretions, looking outwardly very like the pods, capsules, nuts, drupes, and berries of other species. This resemblance to certain fruits is rendered the more pronounced by the development upon the galls of pigments, wax-like excretions, and hairy coverings, but of course they contain no seeds in their interior—only the larvæ of the animals whose excretions produce the changes of form. The wonderful thing is that the metamorphosis of the growing tissue into a fruit-like body is always of the greatest advantage to the animal which has settled in it, since the tissue serves not only for dwelling and food but also for protection against unfavourable weather and against the attack of foes.

It is also a fact of great importance that different animals produce differently shaped galls on the same plant. The Bedeguars produced by *Rhodites Rosa*, the pea-like galls produced by *Rhodites eglanteriæ*, and the clustered protuberances produced by *Rhodites spinosissima* may all occur side by side on the same rose-leaf (see figs. 361^{1, 2, 3}, p. 533). On the same elm-leaf *Schizoneura Ulmi* produces a wrinkled gall, *Tetraneura Ulmi* a pocket-gall, and *Tetraneura alba* a covering gall (see figs. 361^{4, 5, 6}, p. 533). The spherical gall of *Nematus gallorum* and the bladder-like gall of *Nematus vesicator* occur close together on the foliage of the Purple Willow (see figs. 361⁷ and 361⁸), and one sees Oak-leaves on which the small spangle-galls of four different gall-wasps, viz. *Neuroterus lanuginosus*, *numismatis*, *fumipennis*, and *Spathegaster tricolor* are all present together (see figs. 364^{11, 12, 13, 14}, p. 541). It has been shown that some Oaks, for example, *Quercus pedunculata*, may bear as many as 20–30 different forms of gall produced by as many kinds of gall-wasps. The characteristic shape, colour, and hair-covering of these forms of gall is so constant that we can state with certainty what gall-wasps have given rise to them. These facts force us to the conclusion that the fluids

excreted by different gall-producing insects are specifically distinct. It is only in this way that we can account for the fact that the same vegetable protoplasm is incited in one case to produce a fleshy covering gall, in another a hollow pocket, and in a third a closed gall-apple as dwellings for the particular insects concerned.

It should also be mentioned that the same species of insect produces very similar but slightly different galls on different plants. For example, the gall produced by *Nematus pedunculi* on the lower side of the white-haired leaves of *Salix incana* is covered with a white felt of hairs, that which the same gall-gnat produces on the smooth leaves of *Salix purpurea* is smooth; the gall produced by *Rhodites Rosæ* on the light green leaves of *Rosa canina* is pale yellow and somewhat reddened on that side turned towards the sun; that on the violet leaves of *Rosa rubrifolia* produced by the same insect-species is dark violet, &c. These distinctions, though only insignificant, show how certain external characteristics founded in the specific constitution of the protoplasm of different plant-species find expression even in the gall-structures.

These facts confirm the view that the fluids excreted by different species of insects, as well as the protoplasm of each plant species, have a peculiar composition. It is then quite obvious that the alteration which the protoplasm of a species of plant undergoes under the influence of a specific fluid will be subject to definite laws. The protoplasm of the particular plant-cell receives by reason of the alteration, as it were, a new definite constitution with tendencies not the same as before; but since this constitution determines the outer form of the tissue derived from these cells, the tissue itself will become shaped into a particular specific form. These conclusions are of importance with respect to the question of the origin of new species, inasmuch as they throw some light on the processes which lead to the origin of new forms. We can now say that the alteration in the form of a plant only occurs if the constitution of the protoplasm which forms the starting-point of the plant is itself first altered.

The structures known as galls have not the power of maintaining and multiplying themselves, but when their task is ended they perish. In other words, the progeny arising from the seeds of a plant beset with galls exhibits none of the alterations shown by the members or shoots of the parent plant. If, for example, an Oak which is covered with galls is propagated by seeds, the offspring show no trace of the structural alterations exhibited by the branches, foliage, or flowers of the mother-plant. The only change which is perhaps sometimes retained in the offspring is the metamorphosis of the stamens into petals, which has long been known as doubling, and perhaps also the formation of fasciations, &c. in the floral region, as in Cabbages (where it is known as a Cauliflower). Few attempts have yet been made to investigate this matter. My own knowledge of the subject is restricted to some observations made on the Speedwell *Veronica officinalis*. Plants of *Veronica officinalis* which in consequence of the settlement of gall-mites on them produced double flowers in 1877 in the garden of my country house were planted close beside others free from gall-mites and with normal flowers. In the

following year the gall-mites settled on the latter also, and the greater part of their flowers then became double. The same result was obtained after living gall-mites were transferred by me to isolated plants of *Veronica officinalis* with single flowers. These in the following year also bore some double flowers. Fruits with ripe seeds were only produced from the flowers which had remained single amongst the double ones; and the plants which grew up from these seeds always bore single flowers only. The gall-mites disappeared for some unascertained reason—probably they died in the winter. *Veronica officinalis* has only two stamens in each flower, and in the double flowers both these and the two carpels are changed into petals so that of course we could not expect fruit and seeds from them. It would not be impossible, however, that flowers of other plant families which are provided with a large number of stamens might behave differently. It might happen, for example, that only *some* of the stamens would be changed into petals by the gall-mites, and that the carpels would remain capable of fertilization. If on such plants fruits and seeds capable of germination should ripen, the latter might perhaps produce plants with completely and half double flowers. This would be explained by supposing that the alteration undergone by the protoplasm of the cells in the outer part of the flower had extended to the inner, especially to the ovules and seeds, and further to the plants proceeding from these seeds. I would therefore not undertake to state that the Stocks (*Matthiola annua* and *incana*), the Wallflower (*Cheiranthus Cheiri*), the Pinks (*Dianthus Caryophyllus*, *plumarius*, &c.), the Poppies (*Papaver Rhæas* and *somniferum*), various Ranunculaceæ (*Delphinium*, *Pæonia*, *Ranunculus*), and many other plants which have long been cultivated in gardens with semi-double flowers, and which produce such flowers when propagated by seeds, had not gained this characteristic in the first place by the influence of gall-mites. It is less probable, though not beyond the range of possibility, that by the grafting of Hawthorn branches whose uppermost leaves have been deeply segmented by the influence of the gall-gnat *Cecidomyia Cratagi*, a Hawthorn bush might be produced which would exhibit these deep segmentations and slits on all its foliage. However, these last remarks are the merest suppositions; at present we have not the data on which to base any definite conclusions.

THE GENESIS OF NEW FORMS AS A RESULT OF CROSSING.

The aim of agriculturalists has always been so to cultivate their land as to rear plants likely to grow luxuriantly, to bear good fruit, and thus to afford an abundant harvest in return for their pains. Gardeners similarly have made it their endeavour to produce from wild plants races whose flowers are superior to those of the ancestral stock in form, colour, and scent; and the results of their labours are the delight and admiration of all lovers of beauty. In both cases the idea has been to perfect and “ennoble”, and the means adopted have been successful to a degree calculated to amaze anyone who studies the history of cultivated plants with attention. The methods which led to these results have not always been deliber-

ately adopted, nor have they depended on scientific researches. On the contrary, chance observations made by growers in the course of their dealings with vegetable life as it occurs in nature have been the means of suggesting the first unaided attempts to make crops more productive, fruits and vegetables more palatable, and flowering-plants more pleasing to the eye.

The most important method adopted has been the artificial crossing of the species which are brought under cultivation. When we consider that, from time immemorial, Chinese and Japanese gardeners have produced Asters, Chrysanthemums, Camellias, Pinks, Peonies, and Roses, of which the majority are the results of crossing, we may assume with certainty that the practice of dusting flowers of one species with the pollen of another species first came into use in those countries. It is true that in Europe the contrivance was known to rose-growers at the time of the Roman Empire, but it was not employed on an extensive scale till the seventeenth century, when the fashion for breeding Tulips and Auriculas became the rage. The gardeners of that day still made a great secret of their mode of procedure, and it was not till the latter half of the eighteenth century that the production of new forms of plants by the aid of artificial crossing was carried on at all generally. For some decades the rearing of these new forms, which are called *hybrids*, has been one of the most important parts of a gardener's duties, and we shall not exaggerate if we put the number of hybrids hitherto produced in gardens in the course of the nineteenth century at 10,000. Many hybrids which were great favourites only a short time ago have disappeared from our gardens and have been replaced by others. As in so many other matters, the fashion changes; new forms are in constant request, and horticulturists endeavour to meet the demand by introducing wild plants from the most various regions and crossing them with those already under cultivation. It is now no longer uncommon for gardeners, in advertising some plant which has been brought from distant parts, to recommend it to the trade, not on the ground of its own beauty, but because it possesses flowers of an exceptional colour or leaves of a peculiar cut, and will therefore, in all probability, if crossed with other species, yield handsome new hybrids. Rose-growers always welcome the discovery of any instance of variation in the Wild Rose as an important event, because, by crossing this Rose with others, they are able to produce a large number of new forms, and there is always the chance that one or other of them may find favour with the public. On an average, 60 newly-bred Roses come into the market yearly; in the year 1889 the number even amounted to 115! A Rose cultivator at Meidling, near Vienna, grows in his garden nearly 4200 different kinds of Rose, and yet he is still far from possessing all the forms which have been produced in recent times (chiefly by French growers) by crossing one with another. According to his estimate, the number of Tea and Indian Roses alone is nearly 1400, and the total number of all the different Roses which the trade has produced up to the present day amounts to 6400.

The plant-forms which are called into existence by the operation of crossing are, in the case of Roses, reproduced largely by means of brood-bodies (cuttings and

layers) as well as by budding and grafting (see vol. i. p. 213); but the *first origin* of the new forms is always to be traced to crossing. This statement applies also to many other plants of which gardeners have taken possession, and especially to cases where propagation by seed requires more time and trouble than multiplication of brood-bodies. The kinds of Tulip, Gladiolus, and Lily produced by crossing are propagated most easily by means of bulbs, and the tuberous Begonias, Dahlias, and Gesneraceæ by tubers, whilst Pinks, Pelargoniums, Cactuses, and many others are most rapidly reproduced by cuttings. Moreover, these methods ensure the preservation of the peculiarities of the new forms unchanged, and such perpetuation of characteristics would be much more difficult to achieve if the plants were propagated by means of seeds. On the other hand, a number of new forms which have originated as the results of crosses effected in gardens, such as those of *Petunia*, *Portulaca*, and *Viola*, are reproduced with less trouble and greater rapidity by seeds, and that method is in such cases preferred to the cultivation of brood-bodies.

The statement that new forms of plants are bred originally in gardens by any other method than that of crossing is incorrect; it is sometimes made in ignorance, but sometimes also with the intention of deceiving. In former times gardeners believed that, in order to produce new forms, it was sufficient to plant different species in close proximity to one another. The idea was that if the seeds of such plants were taken and sown in good soil, there would always be found amongst the seedlings a few forms differing from the parent; these were to be selected for especial care in cultivation, and were to be treated as starting-points of new forms. The gardeners who acted on this assumption had not, it is true, themselves crossed the flowers; and if this was all they meant, there was no falsehood in the statement. The operation of crossing was, however, performed without their knowledge by hive- and humble-bees and other insects, and the planting together of the different species was only of advantage inasmuch as it facilitated the conveyance of pollen from one species to the stigmas of another. A celebrated grower of the old school once assured me, in all seriousness, that he did not himself cross the plants he reared, but that he had repeatedly observed that early in the morning, soon after a flower opened, it put forth infinitesimally fine threads which radiated in all directions and reached across to the flowers of other plants, forming in a short time a web like that of a spider! I would not have mentioned this statement were it not for the importance of pointing out the unreliable character of so many of the statements made by gardeners, especially in the past; and I repeat that the person responsible for the above communication is a well-known and much-esteemed horticulturalist. Gross inventions such as the above would, of course, be at once seen through and rejected by any thoughtful man; nevertheless, in some instances, reports of growers, likewise untrue or inaccurate, but not bearing the stamp of improbability so plainly upon the face of them, have been credited and have even found their way into books, particularly into those whose authors have omitted to confirm the reports by watching the garden-experiments from beginning to end themselves. The statements are then not infrequently quoted as "results obtained

by trustworthy experiments made by gardeners" and relied upon for the foundation of "laws based upon facts"; theories are then built up upon them, and are copied from one book to another. It becomes very difficult afterwards to get rid of such propositions, especially if they afford support to the hypotheses of distinguished *savants*.

An instructive example of the kind of thing referred to is afforded by the following statement which for a long time obtained currency in works on Botany: "Hybrids resulting from the crossing of two species exhibit two forms, in each case, according as the pollen employed in generating them belongs to the one or to the other species." There are, of course, two ways in which a pair of species, which may be represented by the letters A and B, may be crossed. In one case the pollen from A is transferred to the stigma in B, whilst in the other case the pollen is taken from B and transferred to the stigma in A. Now, it has been asserted that it is possible to determine from the form of the hybrid which of the two parent-species supplied the pollen. The hybrid is said to resemble that parent more closely from which the pollen was derived so far as its flowers are concerned, but to show greater affinity to the fertilized stock in respect of its foliage. This is, however, absolutely untrue. All careful experiments made without prejudice have pointed to the conclusion that it makes no difference to the forms, either of the leaves or of the flowers, whether the pollen has been taken from the one parent-species or from the other. Besides this, in most instances the approximation of the hybrid-form to one or the other stock affects all parts of the hybrid plant in an equal degree, and not the flowers or the foliage only. In the rare cases where a hybrid has flowers more like those of one parent and leaves more like those of the other, it is just as likely for one stock as the other to have yielded the pollen used for the cross.

But it would be a thankless task to attempt to correct all the hasty, careless, and erroneous statements, past and present, and it will probably be of greater utility to give a general survey of what has been ascertained concerning the form and temperament of hybrids by impartial observers who have taken into account all the concurrent circumstances, and have allowed for the sources of error incidental to the experiments.

The formation of a hybrid plant presupposes two stock-plants as parents which have different properties and characters. A cross must take place between the two—that is to say, the stigma of the one must be dusted with pollen from the other; the pollen must put forth pollen-tubes and an effectual union between spermatoplasm and ooplasm must be effected. For the sake of brevity, the plant from which the pollen, and therefore also the spermatoplasm, is derived is called the paternal stock or father-plant, and that which has its stigma dusted and its ooplasm fertilized is called the maternal stock or mother-plant. As a plant's external marks and characteristics, which are perceptible to our senses, are an expression of its internal organization and of the specific constitution of its protoplasm, it may be assumed that the plant-individual which owes its existence to the union of two protoplasts

of different constitutions possesses marks and attributes, some of which are characteristic of the father and others of the mother. As a matter of fact, the individuals which growers call by the various names of hybrids, mongrels, and bastards answer to this supposition. Some of their attributes and external characters are derived from the paternal, some from the maternal stock. If the relative admixture of the two stocks were to be determined in the case of a hybrid by summing up the characteristics transmitted from each source, the share of each parent would in many cases be found to be a half. In such a case it is usual to say that the hybrid is a mean between its parents. Examples are afforded by *Geum hybridum*, which originates from crossing *Geum montanum* and *G. rivale*, *Hieracium stoloniflorum*, derived from *Hieracium aurantiacum* and *H. pilosellaforme*, and *Nuphar intermedium*, a cross between *Nuphar luteum* and *N. pumilum*. But it also happens sometimes that the proportion of characters inherited by a hybrid from one of the parent-stocks amounts to about two-thirds, leaving only one-third as the proportion inherited from the other, and in that case the hybrid is said to exhibit an approximation to one of the parent-species. The Saxifrage hybrids are very instructive examples of this class. The stigmas in a flower of *Saxifraga aizoides* were dusted with the pollen of *S. casia*. Fertilization was successfully effected, and a capsule containing fertile seeds came to maturity. The plants reared from these seeds resembled in some cases the intermediate form described by Botanists under the name of *Saxifraga patens*; others approximated more closely to the paternal stock, and a third group to the maternal stock. A similar result was obtained by crossing a flower of *Saxifraga aizoides* with the pollen of *S. mutata*. From seeds of the same capsule were produced two different kinds of hybrid, of which one was intermediate between the parents (*Saxifraga Hausmanni*), whilst the other (*Saxifraga inclinata*) approximated more closely to *S. mutata*. These experiments point to the conclusion that the share which each parent has in the form of a hybrid depends upon the quantity of its spermatoplasm or ooplasm, as the case may be, used in the production of the seedling relatively to the quantity derived from the other parent; and in the case of hybrids issuing from the same fruit we are forced to suppose that the variability of the degree in which a particular form is inherited is caused by the existence of quantitative differences between the several spermatoplasmic and ooplasmic nuclei (or cells) which coalesce in pairs in the interior of the same ovary.

Important evidence in support of this supposition is derived from experiments made in connection with the crossing of various composites of the Thistle genus (*Cirsium*). In these plants each ovary contains a single ovule only, and therefore each fruit can only produce a single individual. On the other hand, each capitulum is composed of a large number of florets, and when a head is in full bloom nearly a hundred mature stigmas project from it in close proximity to one another. If pollen from another species is transferred by means of a paint-brush on to these stigmas, wholesale crossing, so to speak, ensues and it may be confidently expected that a proportion of these simultaneous crosses will be effectual. The harvest of fruit

from the capitula selected for the experiment was not, it is true, very plentiful, but some fruits invariably came to maturity. If these one-seeded fruits, all of which have originated at the same time and under similar conditions, are sown, the individuals produced from them are but seldom like one another. The attributes and external marks of the paternal and maternal stocks respectively are in some represented in the proportion of about 2:1, in others in the proportion of 1:2, and in a third class in practically equal proportions; cases are even known where four, five, or more distinct forms of hybrid have developed from the fruits of a single capitulum. I found the most striking differences amongst the hybrids obtained by crossing a capitulum of *Cirsium oleraceum* with the pollen from a capitulum of *Cirsium heterophyllum*. Those produced by crossing a head of *Cirsium Pannonicum* with pollen from a head of *Cirsium Erisithales* were scarcely less conspicuously diverse. As it must be presumed that the spermatoplasm and ooplasm—or rather the spermatoplasmic and ooplasmic nuclei—which have been formed in the adjacent florets of a capitulum are alike in composition and ultimate structure, the variety of the hybrids springing from such florets must depend solely on the relation between the masses of ooplasm and spermatoplasm respectively which coalesce in a flower, and the ratio between these masses must be in the one case 1:2, in a second 1:1, and in a third 2:1. Of course these ratios give but an approximate measure of the degree in which each parent has participated in the generation of the intermediate forms. Where five kinds of intermediate forms occur the series would be approximately represented by the ratios 1:4, 2:3, 1:1, 3:2, and 4:1. The first time flowers of a head of *Cirsium Erisithales* were crossed with pollen from *Cirsium palustre* they produced two different forms of hybrid, one of which approximated to the paternal, the other to the maternal stock; but no form exactly midway between the two parent-stocks was obtained. A second trial of the same experiment resulted in the production of a single form which did occupy this intermediate position. These observations show that there is no definite law governing the form of hybrids; one might even say that irregularity is here the rule. On one occasion all the individuals which are the result of a cross between two species are alike, on another occasion they constitute more or less numerous links in a chain of intermediate forms.

Hybrids which do not stand midway between the parent-species but approximate to one or other of them are called *goneoclinic* ($\gamma\omicron\upsilon\epsilon\lambda\iota\varsigma$ =parent, $\kappa\lambda\iota\upsilon\omega$ =I lean). That such hybrids may arise from a first cross is established beyond question by the experiments above recorded; but there is also another process whereby they are produced, and that is the crossing of a hybrid with one of its parent-stocks. These crosses are effected in great numbers, and all observers agree that in general the results are better in such cases than where two species are crossed; that is to say, if a hybrid's stigmas are dusted with the pollen of one of the parent-species a larger number of fertile seeds may be looked for than if the plants crossed were of distinct species. The individuals resulting from the cross of a hybrid with one of the parent-stocks also occupy, as might be expected, a position as regards marks and attributes

intermediate between their progenitors: here again, however, forms are not always alike, and sometimes several intermediate forms make their appearance. If the hybrid derived from *Cirsium Erisithales* and *C. Pannonicum*, which inherits equally from both parents, be crossed with pollen from *Cirsium Erisithales*, the resulting individuals have a stronger resemblance to the latter species and are instances of goneoclinic hybrids. But when *Cirsium Erisithales* and *C. Pannonicum* are crossed for a first time hybrids are also produced which are not exactly midway between the parents but are more like *C. Erisithales*. These naturally resemble the goneoclinic hybrid derived from crossing the offspring of *C. Erisithales* and *C. Pannonicum* with *C. Erisithales*, and if one were not in a position to follow the history of the origin of the hybrid in question its characteristics alone would not furnish sufficient data for a judgment as to the mode of production of the goneoclinic hybrid.

Hybrids which are the offspring indirectly of three different species are called ternary hybrids. The word "indirectly" must be specially emphasized here, lest the reader should fall into the error of supposing it to be possible that pollen-tubes from two or more species should simultaneously fertilize a single ovule. Such an occurrence never happens, not even if a mixture of pollen belonging to two or more different species be placed upon the stigma of a particular flower. On the other hand, it has been ascertained by numerous experiments that if the hybrid-offspring of two species is crossed with the pollen of a third species, or *vice versâ*, another hybrid is produced. Thus, for instance, if the hybrid of *Linaria genistifolia* and *L. purpurea* is crossed with the pollen of *L. striata* the result is a ternary hybrid. In one experiment the stigmas in a capitulum of *Cirsium Linkianum* (the hybrid offspring of *C. Erisithales* and *C. Pannonicum*) were dusted with pollen taken from *C. palustre*. A considerable number of fruits ripened, and the hybrids which arose from them were ternary hybrids, exhibiting marks and characteristics of *C. Erisithales*, *C. Pannonicum*, and *C. palustre* respectively. These hybrids, moreover, were not all alike; some of them bore striking resemblance to *Cirsium aquilonare*, the hybrid produced by crossing *C. palustre* and *C. Pannonicum*, and exhibited very few of the peculiarities of *C. Erisithales*, whilst other individuals were extremely like *Cirsium ochroleucum*, the hybrid obtained by crossing *C. Erisithales* and *C. palustre*, and only showed slight indications of its relation to *C. Pannonicum*. Growers of garden-flowers have achieved great success in producing ornamental ternary hybrids in a number of genera (*Achimenes*, *Begonia*, *Dianthus*, *Gladiolus*, &c.). Ternary hybrids of various Willows are also met with in gardens; one of these is obtained by crossing *Salix Cremsensis*, a hybrid of *Salix Caprea* and *S. daphnoides*, with *S. viminalis*, another by crossing *Salix Wichura* (the hybrid-product of *S. incana* and *S. purpurea*) with *S. cinerea*, and so forth. Willows have been also used for the prosecution of still further experiments. The crossing of two hybrids of different parentage on both sides resulted in the genesis of hybrids combining four species of Willow. Indeed, six different species of Willow have on one occasion been combined by successive crossing—Wichura having

succeeded in producing in Breslau a compound hybrid in which were united *Salix Caprea*, *S. daphnoides*, *S. Lapponum*, *S. purpurea*, *S. Silesiaca*, and *S. viminalis*.

It need hardly be said that the characteristics of the six ancestral species in such a case as that of the last-mentioned hybrid are not easily identified. Even where a hybrid is the offspring of a single cross between two species it is not always easy to determine its origin from its external appearance, and in the absence of any knowledge of the history of its production. The characteristics of the parent-stocks are not combined in all hybrids according to a single definite rule. Sometimes the combination seems to amount to a complete *fusion*, so that the form produced might be compared to an alloy of two metals. Very often a new form is generated which combines in a definite geometrical ratio the characteristics of the parents in respect of the position and direction as well as the shape and size of its separate parts. In that case there is said to be a union of the parental characters. The structural characters of both stocks are represented unmodified, but are so closely bound together as to suggest a composite crystal founded upon two different crystalline forms. Just as in definite combinations of crystals the faces of one component form are dominant, and determine the general aspect in one case and those of the other component form in another case, so in many hybrid plants sometimes the attributes of the one parent, sometimes those of the other, are most conspicuously reproduced. Other hybrids again are analogous to combinations in which both crystalline forms are equally represented. Again, in addition to the above classes of hybrids wherein the parental characters are either completely merged together or intimately united there are many cases where those characteristics are present almost unchanged, and subsist side by side like the particles of a rock. The most common case of this *mixture* or juxtaposition of properties occurs where the hybrid displays hairs, glands, or prickles of two forms interspersed together, one of which is identical with the form of the structure in question exhibited by the maternal stock, whilst the other has been inherited unchanged from the paternal stock. Or, one part of the hybrid's flower may be coloured like one parent and another like the other parent. Hybrids are also known in which the foliage is almost indistinguishable from that of one parental stock whilst the flowers are like those of the other, so that at first sight a hybrid of the kind looks as if it were a plant of the former species with flowers of the second species affixed to it for a joke. On closer inspection some slight differences may be perceived between the leaves and flowers of the hybrid and those of the parent species respectively, but this does not alter the fact that hybrids exist whose leaves resemble far more closely those of one parent, whilst their flowers are more like those of the other. Probably it was the occurrence of such a hybrid which suggested the proposition referred to on p. 557 that in the product of a cross between two species the flowers reveal the paternal and the foliage the maternal stock. But this statement is incorrect, as was said before, for some hybrids approximate to the maternal stock in respect of their flowers, and to the paternal stock in respect of their leaves.

Of the three ways in which the parental characters may be combined in a

hybrid—i.e. by fusion, by union, or by mixture—one alone sometimes prevails in all the parts; but usually, on the contrary, there is an incalculable degree of variation in this connection. There are, for example, Rose hybrids in which the outline of the leaves exhibits a union, the colour of the flowers a fusion, and the hairs a mixture of the corresponding characters in the parents.

A brief account will now be given of a few examples to illustrate the manner in which the combination of parental characters in a hybrid is manifested throughout the structure of the plant and particularly in the forms of the stems, leaves, and flowers, and in those of thorns, bristles, hairs, and other epidermal appendages. The species of Willow known as *Salix Caprea* grows in the form of a little tree, with thick, straight, erect branches, each of which bears about 25 leaves; *Salix repens*, on the other hand, is a low shrub with a procumbent stem and slender, rod-like branches ascending in curves from it, and each bearing about 40 leaves. The hybrid of these two is a small tree with a bent stem and ascending branches, which in length, thickness, curvature, and direction are intermediate between the *Salix Caprea* and *Salix repens*, and which are furnished with some 30 leaves apiece. Again, the foliage-leaves of *Prunella vulgaris* have their margins entire, whilst those of *P. laciniata* are deeply cut, and their hybrid *Prunella intermedia* has lobed leaves. The leaves of *Potentilla sterilis* (or *P. Fragariastrum*) possess three leaflets, each leaflet being furnished on either side with from four to five serrate indentations. The leaves of *Potentilla micrantha* likewise possess three leaflets, but each leaflet has from seven to ten serrate teeth on each side. In the hybrid of these two species the leaflets have from six to eight indentations on each side. The shape of the leaf is, as is well known, intimately connected with the course, ramification, and disposition of the bundles called nerves. Now, if the net-work of strands in the leaves of the parent-species is compared with that in the leaves of the hybrid, it is astonishing to find how the union of the two systems may be traced in the minutest details. No group of plants lends itself better to this sort of investigation than the Willows. Even if a single leaf of the hybrid offspring of two species of Willow is submitted for inspection, it is possible in most cases to determine, from the number and distribution of the nerves, the identities of both its parents. *Salix purpurea* produces one hybrid when crossed with *Salix grandifolia*, and a second when crossed with *Salix Caprea*. *Salix grandifolia* has twice as many lateral nerves in each leaf as *Salix Caprea*, and this difference is reproduced in the corresponding hybrids, whose leaves in all other respects resemble one another closely.

The involucrel leaves of Composites are well known to be extremely diverse in shape, and systematic Botanists have always attributed great importance in the discrimination of species to the size, shape, and margination of these leaves and to the peculiar appendages at their apices. Now, the hybrids of Composites not infrequently have involucrel leaves which differ widely from the forms characteristic of the parent-stocks. Thus, for instance, each leaf of the involucre in a capitulum of *Centaurea rupestris* terminates in a long yellow prickle, whilst the

corresponding structure in *Centaurea Scabiosa* is bordered by a broad, membranous, fringe-like edge of a dark-brown colour. In *Centaurea sordida* (Grafiana), the hybrid offspring of these two species, each involucre leaf is edged with a narrow, light-brown membranous and fringed border, and terminates in a short yellowish prickle. A very instructive example of the union of parental characters affecting all the different parts of the floral region is afforded also by the Labiate *Marrubium remotum*, which is produced by crossing *Marrubium peregrinum* and *M. vulgare*. The small tuft-like inflorescences in the leaf-axils of *Marrubium peregrinum* include from 10 to 18 flowers, those of *M. vulgare* from 4 to 5, and those of the hybrid *M. remotum* from 5 to 10. The calyx of *M. peregrinum* is grey and covered with felted hairs, and its margin is provided with five large subulate teeth which terminate in straight points. The calyx of *M. vulgare* is green and sparsely clothed with hairs, and its edge has ten small teeth which terminate in stiff reflexed points like hooks. Five of these teeth are rather longer than the rest. The calyx of *M. remotum* is greyish-green and clothed with a loose felt; its edge is furnished with five big subulate teeth which terminate in stiff out-curved points, and have from two to five very small teeth interspersed between them. The three lobes of the under-lip of the corolla are almost of equal length in *Marrubium peregrinum*, whilst in *M. vulgare* the middle lobe is three times as long as the two lateral lobes. In the hybrid *Marrubium remotum* the middle lobe of the lower lip is half as long again as the lateral lobes. An excellent example is also afforded by *Dianthus Œnipontanus*, a hybrid Pink resulting from a cross between *Dianthus alpinus* and *D. superbus*. In *D. alpinus* the bract-like scales at the base of the calyx are almost as long as the tube of the calyx itself, whilst in *D. superbus* their relative length is only a quarter or a third; in the hybrid *D. Œnipontanus* these bracts are half as long as the tube. The petals of *D. alpinus* have broad laminæ beset at the margin with short triangular teeth, those of *D. superbus* have their laminæ slit up into a number of narrow strips, and those of *D. Œnipontanus* have deeply-incised laminæ, the margins being divided into linear segments. The dimensions of the various parts of the flower in a hybrid also exhibit in most cases a combination of the corresponding parental characteristics. Thus, for instance, the perianth of the Orchid *Gymnadenia conopsea* has a long spur—that is to say, the segment of the perianth known as the labellum is produced backwards into a saccate protuberance supposed to resemble a spur, and this portion of the petal in *Gymnadenia conopsea* is 15 mm. in length. In *Nigritella nigra*, on the other hand, the spur is very short, measuring about 2 mm. The hybrid of these two Orchids, *Nigritella suaveolens*, has a spur varying from 5 to 7 mm. in length. In Willow hybrids the number of stamens in each flower of the hybrid is invariably between the corresponding numbers in the two parent-species. For example, the number of stamens in a flower of *Salix alba* is 2, in *Salix pentandra* 5–12, and in their hybrid *Salix Ehrhartiana* 3–4.

The cellular structures produced from the epidermis of the stem and leaves which are differentiated as hairs, bristles, scales, glands, &c., and are classed together

under the name of investments (*indumentum*), are very constant characters in most species of plants. The occurrence of stellate hairs, in particular, is looked upon by systematic Botanists as an important point in assisting them to distinguish between similar species, and so also is the presence of glandular hairs composed of simple rows of cells, and terminating in globular bladders full of ethereal oils. Hybrids exhibit the most varied combinations of the indumenta of their parents. In the majority of cases the characteristics of the two stocks in this respect are mixed, but less frequently are they united, and in the latter case the shape, size, and number of hairs, bristles, scales, and glands are intermediate between those of the same appendages in the two parent-species. The Lungwort genus (*Pulmonaria*), which has a special tendency to hybridization, includes only a few species, but each one may be recognized by the nature of its indumentum. Thus, *Pulmonaria officinalis* is distinguished by the thousands of short unicellular prickly hairs, scarcely perceptible to the naked eye, which are interspersed amongst the long scattered bristles on the upper surfaces of the leaves. In *Pulmonaria angustifolia* the leaves are destitute of these minute prickles, but bear on their upper surface a more abundant quantity of straight appressed bristles of equal length. The leaves of the hybrid derived from the two preceding species, viz. *Pulmonaria hybrida*, are richly supplied with long bristles, and interspersed amongst these may be seen a large number of shorter bristles which are about two or three times as long as the prickly hairs of *Pulmonaria officinalis*. A very instructive example is also afforded by the hybrid *Rhododendron intermedium*, which is easily produced by crossing the two Alpine Roses (*Rhododendron ferrugineum* and *Rhododendron hirsutum*). The upper faces of the leaves of *R. ferrugineum* are dark-green, smooth, and shining, whilst their backs are rusty and dull owing to the presence of a dense crowd of tiny scales. The margins are not ciliate. The leaves of *R. hirsutum* are light-green and beset with scattered whitish glands (see vol. i. p. 232, figs. 54⁵ and 54⁶), and their margins are fringed with long hairs. In *Rhododendron intermedium* both kinds of epidermal appendage are displayed side by side. The under surface of the leaf is furnished with brown scales, though not so profusely as in *Rhododendron ferrugineum*, and its edge is fringed with hairs, but not so thickly as in *R. hirsutum*. The same sort of thing occurs in Roses, Cinquefoils, Blackberries, Drabas, Hawkweeds, and many other plants. Where one parent Rose bears only non-glandular and the other only glandular hairs the hybrid is sure to be clothed with a mixture of the two kinds of hairs. Several species of Cinquefoil (*Potentilla*) have stellate or tufted hairs, whilst others are entirely free from them and bear none but simple hairs on their leaves. In hybrids derived from two of these species—one with compound and the other with simple hairs—stellate or fasciculated hairs are invariably intermixed with a large number of simple hairs. A few species of the perennial Whitlow-grasses (*Draba*), which are indigenous to mountainous districts in Central Europe, have rectilinear anvil-shaped hairs, whilst others have three- or four-rayed stellate hairs. In the hybrids which spring from these different species rectilinear and stellate hairs grow together on the same leaf. If the hairs of two parent-species are of the

same form but of unequal length, those of their hybrid offspring have a length which corresponds approximately to the mean between the lengths in the parent-species. Thus the length of the hairs on the backs of the leaves is 0.3 mm. in *Salix aurita*, 1.2 mm. in *Salix repens*, and 0.6 mm. in their hybrid *Salix plicata*. The hairs in *Salix Caprea* measure 0.8 mm., in *Salix viminalis* 0.3 mm., and in *Salix acuminata*, their offspring, 0.5 mm. Whenever one stock is glabrous and the other hairy, one may be quite sure that the corresponding parts of their hybrid will be furnished with hairs, but less profusely than the parent-species from which that particular characteristic is derived. This is the case, for instance, with *Primula Sturii*, the hybrid produced by crossing the glabrous *Primula minima* with *Primula villosa*, which has glandular hairs. The leaves of the latter are thickly covered with these hairs, which vary from 0.1 mm. to 1 mm. in length, and *Primula Sturii* has scattered glandular hairs which measure 0.3 mm. The hybrids obtained by crossing the Purple Willow (*Salix purpurea*) with the Common Osier (*Salix viminalis*) are distinguished by Botanists into two sections, one of which—*Salix rubra*—approximates to the Purple Willow and the other—*Salix elaeagnifolia*—to the Common Osier. The leaves of the Purple Willow when mature are glabrous at the back, those of the Common Osier have small glistening hairs lying appressed to their under surfaces, parallel to the lateral nerves, and measuring 0.3 mm. There are about 1800 of these hairs on a square millimetre. The hairs of the hybrid *Salix elaeagnifolia* are of the same length as those of *S. viminalis*, but there are only about 800 of them to the square millimetre, whilst the hairs of the hybrid *Salix rubra* are somewhat shorter, and there are only 400 to the square millimetre.

Recently the discovery has been made by Wettstein that the form and disposition of the cells and tissues in hybrids is also a combination of the corresponding characteristics in the parent-species. The various species of the Pine genus (*Pinus*) may be distinguished with certainty by the anatomical structure of their needle-shaped leaves, in particular by the thickness of the epidermal cells, the number of the stone-cells lying beneath the epidermis, and the number of the resin-ducts. In the hybrids the anatomical characters of the parents in these respects are united, and the result is indeed often an exact arithmetic mean between the two. Thus a needle of the Scotch Pine (*Pinus sylvestris*) contains from 6 to 10 resin-ducts, that of the Mountain Pine, *Pinus Mughas (montana)*, contains from 3 to 5, and that of the hybrid offspring of the two from 5 to 7 such ducts. The Junipers (*Juniperus*) afford a similar instance. In their case the leaves are distinguished by the various thickness and length of the layer of sclerotic-cells which covers the back of each leaf, by the width of the resin-duct running through the middle of the leaf, and by the number of the cells encasing that duct. In the hybrids, such as *Juniperus Kanitzii*, which is produced by crossing *Juniperus communis* and *J. sabinooides*, there is evidently a union of the parental attributes in the corresponding cellular structures in the leaves. It has also been shown by Hillebrand that in the Wood-Sorrel (*Oxalis*) hybrids also the anatomical characters of the parents are united, but by far the most comprehensive study which has

been made in recent times into the minute structure of plant-hybrids is by Macfarlane. He selected a number of hybrids, and worked through their anatomy from base to apex in the most painstaking manner. He dealt with roots, stems, leaves, and the various portions of the flower, always comparing their various tissues (both as regards size, form, and distribution) with those of their parent-forms. And his result is to confirm what has been written above, though it is obvious he had never read these pages. Amongst the more interesting of his results may be mentioned those on starch-grains. Of course in a great many of the parent-forms uniting to form a hybrid there is no recognizable difference in the size or structure of the starch-grains. But in the genus *Hedychium* (belonging to the family Zingiberaceæ) exceptions to this rule were found. Thus, those of *Hedychium Sadlerianum* are intermediate in form and size between those of its two parents, *H. Gardnerianum* and *H. coronarium*; and those of a hybrid between *H. elatum* and *H. coronarium* exhibited similar intermediate characters.

It is important to note also that the aromatic substances and colouring matters produced in the cells of a hybrid are inherited partly from the maternal, and partly from the paternal stock. As we have several times already had occasion to mention, the various species of the Rose genus may be recognized at once by their peculiar scent. The perfume of *Rosa Centifolia* is the one which in particular is understood by the rose-scent, but it is very different from that of *Rosa alpina*, and the latter in its turn is unlike any of the scents emitted by *Rosa arvensis*, *R. Gallica*, *R. Indica*, &c. *Rosa Nasterana* has a scent strongly resembling that of Pinks, whilst *Rosa lutea* and *R. punica* are notorious for their disagreeable smell. Now the hybrid Roses emit odours in which the scents of the parent-species are merged together in a great variety of ways. Usually the scent of one stock predominates, and there is only a suggestion of the other. Sometimes, however, an entirely new scent is evolved from the fusion of the two, as is the case, for instance (according to Macfarlane), in *Hedychium Sadlerianum*, the hybrid between *H. Gardnerianum* and *H. coronarium*; and, again, in other cases, one of the component odours is intensified and the other is extinguished. The same statement applies to the aromatic substances to which the scent of the foliage is due. The hybrids of *Rosa glutinosa*, *Rosa rubiginosa*, and *R. rugosa*, with *Rosa Gallica* and *R. Centifolia*, are very interesting in this connection. The aromatic substances which are contained in fruits and excite our nerves of taste are also inherited, partly from the maternal and partly from the paternal stock. Owing, however, to the difficulty of naming the various sensations of smell and taste it is of little use to discuss the subject more fully.

As regards the colouring-matters reproduced in hybrids the first point to notice is that in cases where the foliage is of different shades of green in the parent-species the leaves of the hybrid exhibit a shade intermediate between the two. Conspicuous instances of this are afforded by the hybrid Willows derived from *Salix nigricans* and *S. purpurea*. In both these species the foliage becomes black when it withers, and this characteristic is transmitted, though not in its full strength, to the hybrids

which *S. nigricans* and *S. purpurea* form with other Willows whose foliage turns brown when it dries up. The colour of the flowers in hybrids is usually the result of a *fusion* of the colours in the parent-species; less frequently it is a *mixture* of the original colours. The cases of fusion occur especially amongst the hybrids of Orchids, Louseworts, Anemones, Pulsatillas, Medicagos, and Mulleins. If the tone of the red or blue petals in one parent-species is dull and in the other bright, the same colour reappears in the hybrid, but of a medium tone. Thus the colour of the petals in *Gymnadenia conopsea* is rose-red and in *Nigritella nigra* dark blood-red, whilst in their hybrid, *Nigritella suaveolens*, it is bright carmine. The corolla of *Pedicularis incarnata* is of a subdued carmine tint, and that of *P. recutita* of a dark reddish-brown, whilst their hybrid, *P. atrorubens*, has a dark purple corolla. Where the floral colour of one parent-species is white and that of the other a full yellow, red, or blue, the hybrid's flower usually exhibits a pale yellow, red, or blue coloration. The flowers of *Anemone nemorosa* are white, those of *A. ranunculoides* golden-yellow, and those of their hybrid, *A. intermedia*, sulphur-yellow. The colour of the flowers in a hybrid whose parents have yellow and violet, or blue flowers, respectively, is very remarkable. *Medicago media*, which is the hybrid offspring of the yellow-flowered *Medicago falcata*, and the blue-purple flowered *M. sativa* very often has green corollas. The hybrids (*Verbascum commutatum*, *V. rubiginosum*, *V. Schmidtii*, *V. versiflorum*, &c.) obtained by crossing the yellow-flowered Mulleins with *Verbascum phanicum*, whose flowers are a conspicuous purple, all display a bright brown tint in their corollas. The colour in question is just the same as that which is produced by mixing gamboge with the purple prepared from carmine and indigo. Quite a different tint is exhibited by the corolla of *Verbascum pseudophanicum*, the hybrid generated by crossing *V. Blattaria* and *V. phanicum*. One of the parent-species (*V. Blattaria*) in this case has pale yellow and the other (*V. phanicum*) violet-purple corollas, and in the hybrid (*V. pseudophanicum*) the corolla is pale crimson. Nor are cases wanting in which hybrids have been produced from forms with red and blue flowers respectively. The brilliant scarlet-flowered *Dolphinium nudicaule* has been crossed in the Edinburgh Botanic Garden with the dark blue-flowered *D. cashmirianum*, the hybrid product being of a lurid purple-red hue. Darwin obtained by crossing the red and blue Pimpernels (*Anagallis*) a progeny some of which were blue, some red, and some intermediate in colour. As a final instance of this colour-fusion may be cited the hybrid Pitcher-plant *Nepenthes Mastersiana*. This hybrid is produced from *N. sanguinea*, the pitchers of which are of large size and vary in colour from greenish-scarlet to crimson, and of *N. Kharsiana*, which bears long narrow pitchers, varying from yellowish-green to dull red-green. The hybrid (says Macfarlane) presents a corresponding latitude in colour effect, though on the average it is greenish-crimson.

The hybrids which originate from crosses between *Primula Auricula*, whose flower is all of one colour, and *Primula Carniolica*, *P. hirsuta*, *P. Oenensis*, *P. villosa*, &c., which have bi-coloured flowers, are also of great interest in this connection. *P. pubescens*, the hybrid produced by crossing *P. Auricula* and *P. hirsuta*,

is the stock from which the garden Auriculas are derived. The colour of the corolla in *P. Auricula* is a uniform golden-yellow excepting that at the throat, *i.e.* at the junction of the tube with the expanded limb, there is a floury efflorescence which, like that covering the calyx, pedicels, and bracts, is due to a peculiar modification of the epidermis. The corolla of *P. hirsuta* is bi-coloured; the segments of the limb are violet-red, whilst the throat is white. The two tints are sharply marked off from one another, and in consequence a white five-rayed star is seen in the middle of the flower. There is in this case no trace of a floury efflorescence. In the hybrid offspring of these two Primulas both the violet-red of the limb and the white of the throat are blended with yellow; the former exhibits a touch of brown, and in the middle of the flower is a pale-yellow star.

It is much less common for those floral colours which are inherited by a hybrid from the parent-species to be displayed in juxtaposition than in a blended condition. Since the time of the Roman Empire gardeners have crossed the red-flowered *Rosa Gallica* and *R. Damascena* with the white-flowered *Rosa alba* and obtained thereby hybrids in which the petals are striped and spotted longitudinally with red and white (so-called "York and Lancaster" roses). Similar cases occur amongst hybrid Calceolarias, Pinks, Petunias, and Wood-Sorrels, and instances of Tulip and Iris hybrids are also known where the perianths exhibit the two different colours of the parent-species side by side in streaks and patches. A hybrid of *Iris Florentina* and *I. Kochii* is especially deserving of notice. The perianth in *I. Florentina* is milk-white and that of *I. Kochii* is dark violet. The hybrid of these two species was first obtained in May, 1871, in the Botanic Garden at Innsbruck; one of the individual plants thus produced had two of the outer and one of the inner members of the perianth shaped like those of *I. Kochii* and of a deep violet colour, and one of the outer and two of the inner members shaped like those of *I. Florentina* and milky-white in colour. This arrangement of colours re-appeared year after year until in 1877 a single flower, in which the lower white members had some dark violet streaks widening out from the middle to the edge of the perianth also made its appearance. A second plant of the same hybrid developed flowers which only differed from those of *I. Florentina* in that a few of the white petals had dark violet streaks widening out towards the circumference. An equally noteworthy case is that of a hybrid reared in the Botanic Garden at Florence from *I. Germanica* and *I. sambucina*, of which a specimen was sent to me in 1872. One inferior and two superior perianth-members displayed on one half of their surfaces the colour and pattern peculiar to *I. sambucina*, and on the other half those characteristic of *I. Germanica*. The rest of the perianth could not be distinguished except by its smaller size from that of *Iris Germanica*.

It must not be supposed, however, that the presence of variegated stripes, patches, or speckles on petals is always an indication of hybridity. *Viola polychroma*, a very common Alpine species, not infrequently produces simultaneously two, three, or four open flowers, every one of which presents a different mixture of tints, and amongst plants of this species covering only a small patch of ground it

would be easy to find 100 blossoms with corollas differing from one another in the distribution of their colours and in the arrangements of the spots and streaks upon them. Similar phenomena are exhibited by *Iris pumila* and *Polygala amarella*. The flowers in *Polygala amarella* are equally blue and white or sprinkled with blue and white, and it is also no rare thing for plants to bear white flowers interspersed with a few which are sprinkled with blue. In the same way several species of *Anthyllis*, *Euphrasia*, *Galeopsis*, *Linaria*, *Melittis*, *Ophrys*, *Orchis*, *Saxifraga*, &c., exhibit considerable variation in the colours and markings of their petals, which yet is not to be attributed either to hybridization or to the influence of soil or climate. Reference must also be made here to the large number of species (already mentioned on p. 194) in which the floral coloration is by turns blue and white, red and white, blue and red, yellow and white, and so on. Heterochromatism, *i.e.* the change in the coloration and marking of petals, serves, in fact, in some plants as a specific character. Contrasting with these heterochromatic species are those with homochromatic flowers, which, as far as experience has shown, invariably present the same colour and pattern, and only exhibit a slight variation in the depth of the colour when subjected to the influence of light of varying degrees of intensity. *Iris Kochii* and *I. Florentina*, *Primula Auricula*, and *P. hirsuta*, together with other pairs of species referred to above as the progenitors of hybrids of special interest, belong to the category of plants possessing homochromatic flowers, and it is obvious that in the hybrid offspring of such plants the floral coloration would be an important sign of identity.

This will be the most convenient place in which to introduce a few words concerning the *Bizzaria* of Italian gardeners, and also concerning so-called *graft-hybrids*. The name of *Bizzaria* has been given by the Italians to an extremely curious Orange. Galesio (1839) states that this Orange-tree produces at the same time foliage, flowers, and fruit identical with the Bitter Orange (*Citrus Aurantium*) and with the Citron of Florence (*Citrus medica*), and likewise compound fruit, with the two kinds either blended together, both externally and internally, or segregated in various ways. In the fruits of the *Bizzaria* which I have seen, five longitudinal stripes of the colour of a Citron were interpolated in the fruit of the Orange. Other fruits were, on the whole, like Oranges, excepting as regarded an eighth of their mass, which in form, colour, and taste resembled a Citron, and was also peculiar for its extreme convexity. This anomalous segment stretched in the form of a light-coloured cushion from one pole of the spherical fruit to the other. Growers maintain that the *Bizzaria* is the result of a cross between *Citrus medica* and *Citrus Aurantium*, though the gardener who, in 1644, in Florence, raised this tree, declared it was a seedling which had been grafted, and after the graft had perished the stock sprouted and produced the *Bizzaria* (according to which account it would be a graft-hybrid). In other similar cases of *Citrus* hybrids, however, such as the Bergamot Orange, alleged to be a hybrid of the ordinary Lemon and the Bitter Orange, one finds the characteristics of the parent-species do not

reappear in juxtaposition (as in the *Bizzaria*), but are united or fused together. Whether the case of Bergamot Pears, which are striped green and yellow, and that of the half dark- and half light-coloured grapes, of which a few occur occasionally in otherwise ordinary bunches of the fruit, are to be looked upon as parallel phenomena to that of the *Bizzaria* must remain uncertain until it has been ascertained to what particular crosses of the various species of *Pyrus* and *Vitis* the innumerable Pear-trees and Vines now cultivated owe their origin.

Over and over again gardeners have asserted that hybrids may also be produced by budding and grafting, and in order to distinguish plants so arising from those which are the result of a cross (*i.e.* from true hybrids), they are called *graft-hybrids*. One of these plants, a Laburnum named *Cytisus Adami*, which exhibits a curious mixture of the characteristics of *Cytisus Laburnum* (the ordinary yellow Laburnum) and *Cytisus purpureus* in the same individual, has been the subject of lively discussion in scientific circles. It is indeed difficult to imagine anything more curious than a plant of *Cytisus Adami*. Most of the flowers derive their characters equally from both parent-forms; the calyx is not so thickly clad with silky hairs as in *C. Laburnum* nor so smooth as in *C. purpureus*, and the corollas are of a dirty-red colour, compounded of the purple of *C. purpureus* and the yellow of *C. Laburnum*. But the curious thing is that on many of the racemes a few blossoms of different appearance are interspersed amongst these red flowers, some having yellow corollas and silky-haired calices as in *C. Laburnum*, and others, still more remarkable, having half their petals like *C. purpureus* and half like *C. Laburnum*, or a third of their petals like *C. purpureus* and two-thirds like *C. Laburnum*, or some one of many other combinations. According to Schnittspahns, this anomalous form of *Cytisus* was first produced at Vitry, near Paris, in the year 1826, by a grower named Adam, who inserted a bud of *C. purpureus* into a stock of *C. Laburnum*. The shoot which sprang from the bud was not a pure branch of *C. purpureus*, but had characteristics derived both from *C. purpureus* and from *C. Laburnum*. Buds for propagating *C. Adami* were sent from Vitry to gardens all over Europe, and were in some cases inserted into stocks of *C. Laburnum*, and in other cases into stocks of *C. Jacquinianus* and *C. alpinus*. In many cases gardeners grafted buds of *C. purpureus* in addition to those of *C. Adami* on to the same stocks, and thus produced shrubs of most extraordinary appearance. Of the branches some resembled *C. Laburnum*, *C. Jacquinianus*, or *C. alpinus*, others *Cytisus Adami*, and others again *C. purpureus*; and amongst the racemes were many which bore the ordinary flowers of *C. Adami*, interspersed with a few blossoms of *C. Laburnum*, and others in whose flowers a mixture of the properties of *C. Laburnum* and *C. purpureus* was apparent. The fact of main interest, however, is that cuttings from Adam's original plant (the alleged graft-hybrid of *C. Laburnum* and *C. purpureus*) should bear not only flowers of an intermediate type (as might be looked for in a hybrid), but that on certain branches the flowers break back (or revert) to the pure form of one or other of the parents, or that a single flower should exhibit on one half the characters of one parent and

on the other those of the other parent. Thus the alleged graft-hybrid bears three distinct sorts of flowers, and often parti-coloured combinations of the two parent forms. The anatomical details of the tissues of the *Adami*-forms have been examined and compared with those of the two parent-forms by Macfarlane. It appears that the tissues show a remarkable mingling of the two parent-forms. In some the one, in others the other parent-form predominates. Though in the flowers (*ie.* the pure *Adami*-flowers) the mingling is quite consistent with its being a well-balanced seed-hybrid, in the vegetative regions the strikingly diversified intermixture of tissues is unlike that met with in any seed-hybrid hitherto examined. It should be mentioned that where the *Adami*-plant bears *Laburnum* or *purpureus* shoots and flowers the anatomical characters of these shoots is identical with the normal *C. Laburnum* and *C. purpureus*, respectively. Finally the *Adami*-flowers never ripen seeds (the ovules being malformed), though when the parent-forms occur upon it they ripen fruit and seed.

As a general rule the relations of the graft to the substratum (or stock) are very different from those manifested in the case of Adam's experiment. The shoot developed from the ingrafted bud makes the same use of the substratum in which it is imbedded as a parasite makes of its host-plant (see vol. i. p. 213). It procures from the substratum a supply of "crude sap", and this material is absorbed and worked up by the protoplasts of the cells of the graft in the same way as the liquid substances of the soil which are sucked up by roots. It must be premised that those cells of the graft which take up the crude nutrient sap are adapted to their work in very much the same way as are the suction-cells of roots, that is to say, they are able to exercise a selective power, and only admit such substances as are good for the species to which the scion belongs. Any influence that the substratum might have on the graft could scarcely be other than such as would be exercised by soils of various composition. At the most we should expect variations in shape and colour, which have no permanence, and are not retained by the scion's posterity. As a matter of fact, if, for instance, cuttings are taken from an Apricot-tree and grafted on to various other *Amygdaleæ*, or are transferred from a Pear-tree to Quinces, White-thorns, and other *Pomaceæ*, they do not exhibit the slightest alteration in fruit, flowers, or foliage after entering into organic union with the stock. Again, when hybrid Roses produced by crossing are propagated by budding and grafting, the result is the same whatever species of Wild-rose is taken for the substratum or stock. In all the thousands of cases of propagation by these means none has been observed in which the stock has had any essential influence upon the form of the scion.

In 1876 and 1877 certain experiments were made in the Botanic Garden at Innsbruck on the genus *Iris*. They were suggested by the fact of the production of the hybrids of that genus already referred to, and consisted in grafting buds from the root-stock of one species of *Iris* on to that of another species of the same genus. The experiment was attended with perfect success, but the shoots and flowers developed from the ingrafted buds showed no trace of any influence on the

part of the substratum. Buds of *Iris Kochii* grafted on *I. Florentina* produced unaltered plants of *I. Kochii*, and buds of *I. Florentina* grafted on *I. Kochii* developed simply plants of *I. Florentina*. In the Botanical Garden at Vienna there is a male Ginkgo-tree (*Ginkgo biloba*) which, more than a hundred years ago, was the subject of an important experiment. When the tree was still quite small the bud of a female tree was grafted upon it by Jacquin, and a lateral branch was developed from this bud. What we have now is a mighty tree with a number of branches bearing male flowers, and one large branch bearing female flowers. The notable thing about the tree is that the grafted branch follows a course of development which is obviously different from that of the stock. Every year in the spring it puts forth foliage about fourteen days later than the male branches, and in the autumn its leaves are still green long after the rest have turned yellow and, for the most part, fallen off. From this instance we may infer that the shoots developed from the grafted bud adhere with the greatest tenacity even to individual characteristics, and do not suffer the substratum to affect them even in respect of their annual development.

These facts have of recent years led many people to the opinion that the genesis of graft-hybrids is simply a gardener's story, and that even the most famous of the supposed graft-hybrids—*Cytisus Adami*—does not owe its origin to budding, but to a cross between *Cytisus Laburnum* and *C. purpureus*. Still, in view of the curious mixing of the parent-characters in *Cytisus Adami*, as revealed by Macfarlane's investigations, it would perhaps be well to suspend our judgment. It is true that even in true seed-hybrids (e.g. the *Iris* hybrids mentioned on p. 568) a mixing (not a fusion) of the parental characters of the flowers was observed. Fresh observations in this field are wanted, directed especially with a view to showing whether or not the sum-total of the characters of *Cytisus Adami* are absolutely unique amongst hybrid-plants of whatsoever origin.

A further instance of the same nature may be mentioned, as it has been the subject of careful scientific investigation and experiment. In 1876 a Jerusalem Artichoke (*Helianthus tuberosus*) was grafted upon a Sunflower (*Helianthus annuus*) in the neighbourhood of Bristol, and it was alleged that as a consequence the Sunflower stock had acquired from the Artichoke the property of producing tubers on its subterranean portions. Quite lately a series of buds of the Artichoke were grafted on Sunflower stalks by Vöchting, and the results carefully followed. It was not found that the properties of the one were in any instance transmitted to the other, although scion and stock grew together in perfect harmony.

The importance of this subject is so great that I cannot refrain from trespassing for a moment on the domain of Zoology in order to refer to a case which shows that the animal world also sometimes affords instances of the characteristics of both parents being manifested in juxtaposition in their hybrid-offspring instead of being merged together or united in close combination. *Tetrao medius* is well known to be a hybrid produced by a crossing between the Black grouse (*Tetrao tetrax*) and the Capercailzie (*Tetrao Urogallus*). This hybrid is so common in Tyrol that the

poulterers in Innsbruck receive for sale on an average six specimens every year from huntsmen in the immediate neighbourhood. The plumage of some individual examples of *Tetrao medius* is curiously striped with alternate groups of feathers inherited from *T. tetrix* and *T. Urogallus* respectively. In 1879 a huntsman brought me from the remotest part of the Gschnitzthal in Tyrol a hen of *Tetrao medius* whose plumage exhibited a mixture of the feathers of *T. tetrix* and *T. Urogallus*, irregularly distributed in stripes and patches all over the body. The case of this hybrid affords valuable confirmation of the results of the experiments made on *Iris* hybrids, and there can no longer be any doubt of the fact that there are hybrids generated by crossing in which the parental characters reappear in juxtaposition.

In spite of all this, however, I should not like to deny the possibility of the existence of *graft-hybrids*, for there are certain considerations which tend to a contrary conclusion. In most cases the relation to the substratum of those cells of the ingrafted shoot or bud which take the crude nutrient sap from the stem of the stock-plant is just the same as that of a parasite's suckers: they are clearly marked off from the cells of the substratum and are not influenced thereby either in their shape or in their ultimate structure, whilst, conversely, no essential modification is undergone by the substratum through the presence of the graft. There is nothing, however, to exclude the possibility of a fusion between the protoplasmic contents of adjacent cells taking place at the spot where stock and graft unite, and the consequent development of a tissue which is composed of cells arising from a division of the cells containing the mixed protoplasms, and which unites the characteristic features of the tissues belonging to the stock and to the graft respectively. In fact, something of the kind has been observed in the case of the parasitic Balanophoraceæ (see vol. i. p. 194). Now supposing such an intermediate tissue were to be formed at the junction between a graft and its substratum, one or more shoots might spring from it and they would doubtless combine the characteristics of the two species employed as stock and scion.

In relation to the genesis of new forms of plants in nature, the question of the possibility of the existence of graft-hybrids is of secondary importance: but it is of no small moment in connection with the comprehension of the processes involved in hybridization: for, the researches suggested by this problem have led to the conclusion that the marks and attributes of a particular species which are perceptible to our senses are an outward sign corresponding to the ultimate structure and molecular composition of a specific protoplasm, and that wherever the special characters of two species are united in a single plant-form, that form is built up from protoplasm which owes its origin to a combination of the protoplasms of two parent-species.

It is only by adhering to this train of thought that one is able to understand how it is that, also in the matter of chronological development, the vital manifestation connected with the shape, anatomical structure, scent, and colour occupy in hybrids a position intermediate between the corresponding manifestations in the parental species. In the Botanic Garden at Vienna there has been for many years

a Buckthorn-shrub, named *Rhamnus hybrida*, which sprang from a cross between *Rhamnus alpina* and *Rhamnus Alaternus*. One of the parent-species, *R. alpina*, has deciduous foliage, *i.e.* leaves which are green in the summer and wither and drop in the autumn; the other, *R. Alaternus*, has evergreen leaves, which last through the winter and remain on the branches for two years. The hybrid, *R. hybrida*, possesses leaves which do not fall off in the autumn, nor yet last fresh and green for two years, but which maintain their verdure through one winter and fall in the spring when new shoots are sprouting from the buds. The behaviour of hybrids as regards their season of flowering is also very remarkable. From 1863 to 1874 I kept notes concerning the flowering of some fifty different kinds of Willow, growing in the Botanic Garden at Innsbruck, and each year made an entry of the day on which the first flower opened in each plant, whether a pure species or a hybrid.

EARLIEST DATE OF FLOWERING OF A NUMBER OF WILLOWS GROWING IN THE
BOTANIC GARDEN AT INNSBRUCK.

(The date given is the average for 12 years.)

Salix Cremsensis -	March 17	Salix Caprea - -	March 16	Salix daphnoides	March 18
" Mauternesis	" 23	" Caprea - -	" 16	" purpurea -	April 7
" attenuata -	" 25	" Caprea - -	" 16	" grandifolia -	March 27
" Wimmeri -	" 26	" daphnoides	" 18	" incana - -	April 17
" Austriaca -	April 3	" grandifolia -	" 27	" purpurea -	" 7
" Seringeana -	" 3	" Caprea - -	" 16	" incana - -	" 17
" capnoides -	" 5	" cinerea - -	April 10	" incana - -	" 17
" intermedia -	" 6	" grandifolia -	March 27	" incana - -	" 17
" rubra - -	" 6	" viminalis -	April 3	" purpurea -	" 7
" Kernerii - -	" 10	" viminalis -	" 3	" incana - -	" 17
" Oenipontana	" 12	" purpurea -	" 7	" incana - -	" 17
" auritoides -	" 14	" purpurea -	" 7	" aurita - -	" 19
" Fenzliana -	" 21	" retusa - -	" 21	" glabra - -	" 21
" retusoides -	" 21	" retusa - -	" 21	" Jacquiniiana	" 21
" alpigena - -	" 23	" retusa - -	" 21	" hastata - -	" 27
" excelsior -	" 23	" fragilis - -	" 13	" alba - -	" 27
" Ehrhartiana	" 29	" alba - -	" 27	" pentandra -	May 6

The name in the first column is that of a hybrid in each case, and the names on the same line in the second and third columns are those of its parent-stocks.

The above table, which gives the means of the dates recorded in 12 years of the first opening of the male flowers in 15 species and 17 hybrids produced from them by a variety of crosses, shows that the hybrids invariably flower on days between those on which the parent-species enter upon that stage of development. It will be observed that the two alpine Willows, *Salix retusa* and *Salix Jacquiniiana*, flowered on an average in the 12 years on the same day, and that their hybrid *Salix retusoides* kept also to that date.

We have hitherto dealt with those of the marks, attributes, and vital phenomena manifested by hybrids which are derived partly from the one parent-species and partly from the other, and we must now pass to the consideration of such characteristics as cannot be attributed to inheritance from those species. There is, in the first place, the fact that the majority of the hybrids produced from crosses develop

with striking rapidity and exuberance; they not uncommonly flower the very first year after they are sown, whereas the seedlings of the parent-species may not attain to the flowering stage for two or three years; and in respect of the size of the foliage, and still more that of the flowers, hybrids often exceed both parent-species. The latter circumstance is indeed one of the chief reasons why growers make such frequent use of the process of crossing. They are thus enabled to meet the demands of connoisseurs, who prefer to have plants with conspicuous flowers in their gardens. The augmentation in the size of the flowers usually ceases after the first, or at any rate after the second year. Subsequently, the flowers of hybrids become smaller again. On this account gardeners are in the habit of producing such hybrids as are especially valued for their large flowers over and over again by the original method. Of the large number of observations recorded on this subject we will here mention one as an example. *Isoloma Decaisneanum* of the order Gesneraceæ is the product of a cross between *Isoloma Tydium* and *Isoloma sciadocalyx*. The seeds obtained after crossing germinate early, and the seedlings develop rapidly into exceptionally robust plants. The foliage-leaves are three times as large and the flowers twice as large as those of the parent-species; in addition, the flowers are much more numerous than on the parent-plants, and in consequence the hybrid has a much more imposing and showy appearance than either of its progenitors.

Many plants which grow on soil rich in humus in mountainous regions, such as the Lungworts (*Pulmonaria*) and Primulas (*Primula*), do not thrive particularly well in gardens, and certain species die after a short time even when cultivated with the greatest care. Yet the hybrids of such species flourish wonderfully well under similar circumstances. They blossom luxuriantly, and may be kept in a state of vigorous growth for many years. Examples of this are afforded by *Primula pubescens* and *Primula Venzoi*. One of the parent-stocks of *P. pubescens*, viz. *Primula hirsuta*, can only be reared if the soil used is expressly prepared for itself, and if several other special precautions are taken, whereas the hybrid, *P. pubescens*, grows exuberantly in ordinary garden-soil. The case of *P. Venzoi*, the hybrid-offspring of *Primula tyrolensis* and *Primula Wulfeniana*, is still more remarkable. Although both the parent species are reared with difficulty, even when the greatest care is bestowed upon their cultivation, *Primula Venzoi* will flourish with extreme luxuriance if planted close to them in the same soil and under the same external conditions.

Another phenomenon sometimes exhibited by hybrids is a change in the distribution of the sexes. It often happens, for instance, that hybrids produce pseudo-hermaphrodite female flowers and pseudo-hermaphrodite male flowers (cf. p. 294), even where both parent-species have true hermaphrodite flowers. In Willow hybrids a partial transformation of male into female flowers, and *vice versa*, has been not infrequently observed, and we then have monœcious catkins bearing flowers, half of which are female and half male. This change also occurs in true species, but only as a rare exception, whilst in the case of hybrids it is by no means uncommon.

Hybrids also exhibit the phenomenon known as the "doubling" of flowers, which depends upon the transformation of stamens into petals, independently of the action of tiny gall-mites, which are the frequent cause of doubling in other plants (*cf.* p. 548). Several hybrid Roses, Pinks, and Camellias are only known with double flowers.

It is difficult to explain the fact, repeatedly confirmed by observation, of the appearance in hybrids of characters which are not present in either parent-species, or rather which cannot be traced to inheritance from either of those species. Thus it sometimes happens that individual plants of a hybrid develop sinuate foliage-leaves with wavy outline, though in both of the parent-species the leaves are either entire or only slightly toothed. The hybrid *Salvia sylvestris* occasionally exhibits deeply sinuate radical leaves, whilst *Salvia nemorosa* and *Salvia pratensis*, the two species to which it owes its origin, never do so. Another instance of the same kind is that of a Stock, the hybrid of *Matthiola incana* and *Matthiola Maderensis*. Neither the one nor the other parent-species has sinuate leaves, yet here and there plants of the hybrid display foliage with the margins so deeply cut as to remind one at first sight of *Matthiola sinuata*. Again, in *Primula pubescens* the leaves are sometimes more deeply sinuate than in either *Primula Auricula* or *Primula hirsuta*. In hybrids of the Foxglove genus (*Digitalis*), flowers not infrequently make their appearance wherein the corolla is produced underneath into a spur as in the Toad-flax (*Linaria*). One hybrid produced by crossing two species of Water Lily, *Nymphaea Lotus* and *Nymphaea dentata*, displayed dark violet lines on its sepals which are not to be seen in either parent-species. Reference must also be made to the comparative frequency with which hybrids bearing white flowers spring from species with blue, violet, red, or yellow blossoms whose non-hybrid offspring only produce colourless flowers on very rare occasions. Lastly, we may mention the fact that as from species so also from hybrids varieties may be formed; but they have no permanence amongst the descendants of a race, passing into other varieties whenever it undergoes the restrictive influence of a change in external conditions.

3. THE ORIGIN OF SPECIES.

Genesis of New Species.—Derivation of Existing Species.—The Sub-divisions of the Vegetable Kingdom.

THE GENESIS OF NEW SPECIES.

It is now more than forty years since I discovered, on an island on the Danube not far from the little town of Dörenstein, a Willow which had till then remained unknown to Botanists. The plant in question was growing on the island in company with a number of other Willow-trees and Willow-shrubs belonging to the

species known as *Salix incana* and *Salix daphnoides* respectively, and it was apparently intermediate in form between those two species. The hairs, the system of ramification, the foliage, and the flowers resembled those of *S. incana* in some respects and those of *S. daphnoides* in others, and a single glance would have led any unbiassed observer to conjecture that he had to deal with the product of a cross between these two species.

This discovery,¹ made in one of the first years of my career as a student of Botany, chanced upon a time when Botanists were beginning to take a particularly keen interest in all cases of intermediate forms observed growing in a state of nature. Some of the leading men at that time refused to believe in the existence of any wild hybrids, and were of opinion that the supposed cases were *varieties* of species whose presence was to be explained by a tendency in the plant itself to change its form. They also held the view that all plants between which one or more intermediate forms had been found to exist were to be included in a single species, and, in accordance with this, they not infrequently treated three, four, or more kinds of plant previously classed as distinct species as being really "varieties" of a single species, because forms obviously intermediate between them, *i.e.* so-called "transitional forms", had been discovered. This practice was carried so far that several systematic Botanists of that day included in one species 5, 10, and even 15 distinct Hawk-weeds which had been previously described as separate species, the reason for the change being that they were all linked together by transitional forms. Another school of Botanists, on the other hand, recognized in most of the so-called transitional forms the results of natural crossing, but they did not deny the existence in plants of a capacity to form varieties in the Linnean sense in response to changes of soil or climate.

To my mind even at that time there could be no doubt which of the two opposing theories concerning the genesis, significance, and position of intermediate forms was to be preferred. The discovery of the hybrid Willow referred to led to my paying particular attention to plant-hybrids, and in the course of the last forty years I have made extensive series of experiments to clear up many obscure points, and to correct the prejudices which then prevailed.

One misconception as to the nature and significance of hybrids, which had great weight and found expression in the name of "bastard" assigned to them, consisted in the idea that they were contrary to nature. The German word "bastard" is defined by Grimm as a base and useless species. This prejudice was carried so far that Kant positively denied their independent existence, and believed they must necessarily die out with the first generation. Connected with this notion was another, according to which hybrids were destitute of the power of producing fertile seeds and propagating their kind sexually. It probably arose from observation of the hybrids of the Mullein genus (*Verbascum*), which in Central Europe are so common

¹The little paper recording the finding of this Willow, with some additional remarks, by Anton Kerner, was published in 1852 (Vienna, Zool. Bot. Ver. Verhandl. II., 1852). This seems to have been Kerner's second definite contribution to science; what would appear to be his first is printed in the same publication a few months previously.

and conspicuous that they were accepted as the results of crosses between two species even by those amongst the earlier Botanists who were most disinclined to recognize the existence of plant-hybrids. Now, these Mullein hybrids do not for the most part mature any seeds. The pistil itself is usually incompletely developed, and even if one or other of the fruit-capsules does develop, the ovules in it are abortive and infertile. Nevertheless it would be erroneous to say that no Mullein hybrid has ever produced seeds capable of germination. Two such hybrids were artificially generated in my garden, viz.:—*Verbascum rubiginosum*, by crossing *Verbascum Austriacum* with the pollen of *Verbascum phaniceum*, and *Verbascum pseudophaeniceum*, by crossing *Verbascum Blattaria* with *V. phaniceum*. The former of these hybrids, it is true, never produced seeds capable of germination: but in the case of the second, although most of the capsules were empty and abortive, a few containing fertile seeds ripened; so that even the hybrids of Mulleins are not invariably sterile.

Anyone who will look beyond the limited range of that particular genus will be convinced that in respect of their capacity for sexual reproduction hybrids do not differ essentially from plants which have been admitted to be “true”, permanent species by Botanists of all periods. For the case of a few of these true species, as, for instance, *Cochlearia Armoracia*, *Crabætataria*, *Lilium bulbiferum*, *Lysimachia Nummularia*, *Rubus odoratus* and *R. Nutkaensis*, it has long been known that if the stigmas are dusted with pollen from the stamens in the same flowers very few seeds, if any, are set, whilst pollen from other flowers is obviously preferred by them. On the other hand, there are true species whose flowers are pseudo-hermaphrodite, i.e. they have the appearance of being bisexual, but are really unisexual (cf. p. 294). In one individual we find that the ovaries are fully developed, as also the stamens, but that no pollen capable of fertilizing ovules is produced in the anthers; in another plant the ovaries are imperfectly developed, whilst the anthers are filled with effective pollen. For seeds to be set in such circumstances two individuals at least are requisite, and pollen from a plant bearing pseudo-hermaphrodite male flowers must be transferred to the stigmas of the pseudo-hermaphrodite female flowers. Now *hybrids* with pseudo-hermaphrodite flowers also exist, and in their case, as in that of true species, two kinds of individual are requisite to produce seeds capable of germination. Supposing, however, in such a case that the two kinds of plant necessary for reproduction do not grow close together or do not flower simultaneously, or that one of them is altogether absent—a contingency which must often occur—fertilization cannot be effected, and consequently no seeds can be formed. It is scarcely necessary to amplify the proposition that dioecious hybrids behave in this respect in the same manner as true species, and that pollination and fruit-formation may in them be impeded likewise by dichogamy or by heterostylism. In many hybrids, again, as in true species, the relative positions of stamens and pistil, the height of the stigma, the length of the filaments, and other conditions of the kind are not conducive to autogamy, and consequently no transference of pollen from the anthers to the stigmas in the same flower can take place

either at the beginning or at the end of the period of bloom. Such hybrids are dependent upon foreign pollen, and if none is brought at the right time by wind or insects no pollination or fertilization takes place, and no seeds are developed.

Even these brief references to recently-discovered phenomena connected with fertilization are sufficient to indicate that the suppression of the function of fruit-formation in hybrids is due in most cases to the same causes as operate on true species. Innumerable experiments have proved that if at the proper time pollen of the right sort is placed upon the stigmas of hybrids fertile seeds are developed as in the case of true species.

We must now consider a statement which for long held its place in Botanical works owing to the positive manner in which it was enunciated by an eminent authority. The proposition in question, whilst admitting the fertility of hybrids, asserted that it was conditional on the stigmas being supplied with pollen from one or other of the parent-stocks, and that no fruit was formed as a result of autogamy. This assumption rested partly on certain series of experiments performed on garden-plants by the Botanist Koelreuter in the second half of the eighteenth century.¹ By crossing two species of Tobacco-plant (*Nicotiana rustica* and *Nicotiana paniculata*) Koelreuter produced a hybrid which in its characteristics was an exact mean between the two parent-species. The stigmas in the flowers of this hybrid were then dusted with pollen from one of the parents, and the result of this second cross was another hybrid, the characters of which resembled those of the species which supplied the pollen more closely than was the case with the first hybrid. The same treatment was applied to the second hybrid, and thus, after three generations, a plant was evolved completely resembling the male progenitor. The first hybrid had, therefore, in a sense, "reverted" to that particular parent-species. The "reversion" of the hybrid to the other parent-species was similarly procured after three generations. Such a result could naturally not have ensued if the action of the pollen of the parental stocks on the hybrid had not been entirely effectual. It is accordingly quite true that hybrids are fertile when the pollen used to fertilize them is taken from either of the parent-species, but the further assertion that they are sterile if their own pollen is employed for the purpose is incorrect, at any rate as a universal proposition. Koelreuter's own conscientious experiments show conclusively that it is possible for hybrids to bring fruits to maturity as a result of autogamy, and that, as a matter of fact, the majority do develop such fruits. We may also refer to the large number of plants with ornamental flowers, such as Begonias, Pansies, and Pinks, which every year in our gardens produce seeds autogamously, and are reproduced in great numbers by means of those seeds (see p. 556). Some interesting experiments have also been made on *Medicago media*, the hybrid of *Medicago falcata* and *M. sativa*. This plant, which is, in many places, cultivated on a large scale for fodder, is propagated continuously by seeds which are in a very

¹Joseph Gottlieb Koelreuter (1733-1806) was the first to investigate the question of hybridization scientifically and thoroughly. His work, which ranks with the best of modern times, is contained in his *Vortufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen* (published 1761-1766); a convenient reprint was issued in 1893.

subordinate degree, if at all, dependent on the parent-species for their production. Nay more, it would be prejudicial were one of those species to supply the pollen seeing that the fertility of this hybrid is diminished thereby. We have here a case of a hybrid manifesting enhanced fertility as compared with one of its parents: for *Medicago falcata* is one of those Papilionaceæ in which autogamy is attended with very small result. It has been ascertained that in cases where the flowers of that species are thrown upon their own resources for pollen, out of every 30 flowers only two or three fruits containing seeds capable of germination are matured. If flowers of *Medicago falcata* are crossed with pollen belonging to another species, such as *Medicago sativa*, a much larger number of fruits is produced, and it is stated that the number of seeds is almost doubled. *Medicago media* usually sets from six to eight pods in each raceme if the flowers depend upon their own pollen for fertilization. If, however, pollen is brought to them from *Medicago falcata* the degree of fertility is strikingly reduced: the flowers so crossed either remain quite empty or develop pods whose seeds are not capable of germination. *Medicago media* is therefore an instance of a hybrid which is actually injured by being crossed with one of the parent-species, but is successfully reproduced by autogamy. The upshot of all these experiments is that the results of autogamy are no different in hybrids from what they are in species.

We may infer from the same experiments in what way reversions of hybrids to their parent-species should be regarded. Botanists possessed with the idea that every hybrid was the product of some process contravening the laws of nature imagined that this anomaly must be counteracted, and that this was effected by a tendency existing in the hybrid's descendants to approximate sometimes to one and sometimes to the other parent-species, so that in the course of a few generations they would completely revert to the form of a true species. As the accounts given by gardeners seemed to confirm the fact of the occurrence of such reversions, no doubt was raised as to the soundness of this view. The reports of gardeners on the subject were, however, founded on inaccurate observation, want of knowledge, and self-deception. In former years the phenomena of pollen-transport in the case of pseudo-hermaphrodite, dichogamous, and heterostyled flowers, and many other things connected therewith, were not appreciated at their full value; to most gardeners they were altogether unknown, and it was only in the rarest instances that any measures were taken to preserve the species and hybrids reared in gardens from extraneous pollen. The majority of growers had no suspicion that the fruit formed on a particular cultivated hybrid might be due to the effect of pollen conveyed by the wind or by insects from one of the parent-species flourishing in the vicinity, and if they noticed that the seedlings arising from that fruit exhibited characteristics approximating to either of the parent-species they were in the habit of calling the phenomenon a reversion. But if a gardener takes care that the flowers of a hybrid under cultivation are only supplied with pollen developed in flowers of their own kind whilst that of other species is excluded, the plants which arise from the seeds of the hybrid exhibit the characters of that hybrid unaltered. Thus,

hybrids prove true to seed, to use a gardener's expression, and there is no truth in the assertion that they have an innate tendency to revert to one of the parent-forms.

At one time the attempt was made to distinguish two sorts of hybrids—those arising between *species*, which were regarded as sterile, and those arising between *races*, which were regarded as fertile. By "races" are understood forms which, whilst not differentiated by characters of sufficient importance to rank as species, are yet reproduced by seed and transmit their characters to their offspring. They seem to stand midway between what are called varieties and sub-species. Forms arising by the crossing of species were termed hybrids, those arising by the crossing of races "blendings". But in this matter Botanists argued in a hopeless circle. Firstly, it was said that if races were crossed the intermediate forms were fertile; whilst those springing from species were sterile; and, secondly, the distinction between races and species was defined as consisting in the fact of the fertility of the intermediate forms produced by crossing races, as compared with the infertility of those derived from crosses between species. A distinction founded on such reasoning as this is, of course, destitute of any value or meaning. What, then, is the difference between races and species? There are certain forms which have a similar physiognomy, an agreement in certain striking particulars. They are bound together by these common characteristics into a single group, and it must be supposed that they are nearly allied in respect of their origin also. But no more than *affinity* can be predicated by characters which, though perhaps less striking than the others, are yet transmitted unmodified to descendants and prove themselves to be constant attributes. It has been sought to apply the term "races" to nearly akin forms of the kind. But the degree of variation has nothing to do with the conception of a species: the essential point is that the characters wherein the variation is manifested are transmitted unchanged to the descendants, and this happens as a fact in all the cases to which the name of race has been affixed. The use of the term would obviously imply quite a different connotation of the name of species from that which Linnaeus, with logical exactitude, attached to it. According to him a species was not an assemblage of individuals of the same form, but an assemblage of individuals of different forms, constituting a group of units and not itself the unit of the system. If, like the French system, we were to distinguish the groups of nearly allied species as "*petites espèces*" from those exhibiting more marked differences and less nearly akin to one another, which would be known as "*grandes espèces*", that would involve quite sufficient recognition of the difference which exists in various degrees between members of the two categories in question; but the introduction of the word "race" side by side with the word "species" suggests the idea of some line of demarcation between the two such as does not in reality exist. Again, if there is no definite boundary between race and species the separation of blendings from hybrids also fails, and with it the proposition that only those hybrids are fertile which are the offspring of races.

In respect of fertility, then, there is no difference between hybrids and species.

In the one as in the other we find those floral contrivances for bringing about cross-fertilization in the first place and autogamy in the second, of which an account was given in the first part of this volume; in the one case as in the other cross-fertilization often takes place as a result of those contrivances, and both categories include forms which are incapable of self-fertilization, and only develop fruits and fertile seeds in consequence of geitonogamy or xenogamy. Seeing that it has been ascertained also that, provided the pollen from other species is excluded, hybrids transmit their form unchanged to their posterity, and that the substitution of brood-bodies for fruits as a means of reproduction and the enhancement of the development of those bodies in the event of there being no fruit, are phenomena common to species also, we come to the conclusion that no line of demarcation between hybrids and species exists in respect of the function of propagation.

The consideration of all these facts led me years ago to raise the question whether hybrids could originate species,¹ and to answer it in the affirmative. Looked at from this point of view, the hybrids which have been and are being produced in nature acquire a special significance, and it becomes important to form a correct notion as to their existence, behaviour, and distribution in localities where the life of plants is untrammelled and undisturbed. Only the vegetation of Europe has been thoroughly studied in this connection, yet this alone affords a fund of information, and we may take it for granted that what is true for Europe will apply likewise to the other quarters of the globe.

We shall be rather below than above the mark if we estimate at a thousand the number of wild hybrids belonging to the Flora of Europe which have been brought to light during the last forty years. Of these only a small proportion are of the class of Cryptogams, but this circumstance is due to the fact that it is only lately that Botanists have paid any attention to hybrid Cryptogams. Future researches will no doubt establish the hybrid nature of many so-called "transitional forms". Amongst Mosses in particular, several hybrids arising from species which grow in ditches and marshy places (*Hypnum aduncum*, *H. pluitans*, *H. lycopodioides*, &c.) have been discovered. A few hybrids of the genera *Orthotrichum*, *Grimmia*, *Physcomitrium*, and *Funaria* have also been identified. Fern hybrids are known in the genera *Aspidium*, *Asplenium*, *Ceterach*, *Polypodium*, and *Scolopendrium*. *Scolopendrium hybridum*, which was observed in Istria, is especially remarkable as being the result of a cross between two species possessing widely different forms and included in different genera. The parent-species of this hybrid are, firstly, *Scolopendrium officinarum*, which is glabrous and grows in clefts in damp, shady rocks and walls; and, secondly, *Ceterach officinarum*, which has the under surfaces of its fronds thickly covered with brown scales and flourishes in the crevices of dry walls exposed to the sun. Amongst the Horse-tails we may mention *Equisetum inundatum*, a rather common hybrid, which owes its existence to the crossing of *Equisetum arvense* and *E. limosum*.

In the division of the Coniferæ no less than seven hybrids have been recently

¹ Oesterreich. botanische Zeitschrift xxi. p. 34 (1871).

identified, and this fact is of no little significance when taken in connection with the circumstance that Europe only possesses 41 species of Conifers. *Juniperus Kanitzii*, the hybrid offspring of *Juniperus communis* and *J. sabinoides*, is a very instructive instance owing to the great diversity in the form of the two parent-species.

Comparatively few hybrids occur amongst Grasses. The majority belong to the genus *Calamagrostis*. Strangely enough, most hybrid grasses have arisen from crosses between species of different genera, as, for instance, *Festuca* and *Lolium*, *Triticum* and *Elymus*, *Triticum* and *Egilops*. The hybrid derived from *Egilops orata* and *Triticum sativum*, and known by the name of *Egilops triticoides*, and the hybrid *Egilops speltaformis*, obtained by crossing *Egilops triticoides* with *Triticum sativum*, have been the subject of lively discussion in their time, and have contributed not a little to clearing up our ideas concerning hybrids. As a set-off to the Grasses, the groups comprising Reeds, Rushes, and Sedges include a comparatively large number of hybrids. For example, in the genus *Carex* instances have been discovered in the most widely different localities.

Amongst Liliflores and Irideæ only a few wild hybrids have been found, but on the other hand a large number occur amongst Orchidaceæ all over Europe. It is striking how many of these Orchid hybrids spring from species which are placed by Botanists in different genera. Hybrids are known, for instance, which are derived respectively from *Aceras* and *Orchis*, from *Anacamptis* and *Orchis*, from *Caloglossum* and *Orchis*, from *Gymnadenia* and *Orchis*, from *Himantoglossum* and *Orchis*, from *Serapias* and *Orchis*, from *Gymnadenia* and *Nigritella*, and from *Epipactis* and *Cephalanthera*. The hybrid *Epipactis speciosa*, lately discovered in the Erlafthal of Lower Austria, is the result of a cross between *Epipactis rubiginosa* and *Cephalanthera alba*, and is of special interest on account of its manifesting characters strongly resembling those of species indigenous to regions at a great distance from the place where the hybrid occurs, for at first sight *Epipactis speciosa* might easily be taken for *Epipactis gigantea*, which is a native of North America, or for the Japanese species named *Epipactis Thunbergii*.

Hybrids are comparatively numerous amongst the Pond-weed group (*Potamogeton*). These are aquatic plants which discharge their pollen in the form of clouds of dust, and at the season of pollination raise their flowers above the surface of the water. Owing to their being completely protogynous (see p. 310), autogamy is out of the question. The crossing of pairs of species is especially promoted by the circumstance that the different species flower in definite succession, so that always just at the time that one species is terminating its period of bloom another is coming into flower.

Plants which have their flowers in catkins (*amentaceous*), such as Oaks, Birches, Alders, Poplars, and Willows, produce an uncommonly large number of hybrids. In Willows pollination is effected by insects, in the other genera by the wind. This gives occasion for us to raise, in connection with this group, the question whether hybrids originate more frequently from entomophilous or from anemophilous plants.

The fact that many more than a hundred Willow hybrids are known looks as if the agency of insects were the more favourable to hybridization. At the same time we must bear in mind that the number of species of Willow in Northern and Central Europe is very large, whilst the number of different Birches, Alders, and Oaks is small. Taken in relation to the number of species, the hybrids belonging to the plants last mentioned are no less numerous than those of Willows, and it appears, therefore, that hybrids occur as frequently amongst plants whose pollen is dispersed in the form of dust as amongst plants with adhesive pollen which is transported by insects. The prevalence of hybrids amongst Pond-weeds points to the same conclusion. A comparison between the Docks and Polygonums even indicates that in anemophilous plants, such as the Docks, hybrids come into existence more readily than in the case of entomophilous plants as represented by the Polygonums, for in scarcely any genus is the number of hybrids so great in proportion to the number of species as in the Dock genus, and the ratio is certainly higher than it is with the Polygonums.

As regards the Caryophyllaceæ it is remarkable that *Dianthus* has many hybrids and *Silene* few, although these two genera resemble one another in the distribution of their sexes and in being chiefly visited by lepidopterous insects. In the genus *Viola* hybrids are extremely common. It has been shown that many *Violas* which were formerly designated as "transitional forms" are in reality hybrids, and thus the grounds upon which systematic Botanists treated whole series of species as one only are removed. As with the *Violas* in Central Europe so also with their allies the *Cistus* in the South, hybrids are numerous; several kinds of *Cistus* hybrids occur so commonly that they were described as species by the Botanists of former times.

It is noticeable in the Cruciferae that no hybrids are formed in nature between the numerous annual species of this family. There are also only a few hybrids known which are derived from the perennial species. The genera *Roripa* and *Draba* are, however, exceptional in this respect. The case of Ranunculaceæ is similar. In the comprehensive genera *Aconitum*, *Helleborus*, and *Ranunculus*, only a few hybrids have been identified with certainty, whilst in *Anemone* and *Pulsatilla* there are almost as many hybrids as species. The case of the hybrid Water-lily *Nuphar intermedium* will be discussed later on.

Many hybrids are known in the genera *Tilia*, *Hypericum*, *Malva*, *Rhamnus*, *Pistacia*, *Acer*, *Euphorbia*, and *Epilobium*, the last alone including fifty different kinds. This makes it all the more remarkable that so varied a family as the Umbelliferae yields very few hybrids. Of the numerous hybrids belonging to the Saxifragaceæ we may mention as specially noteworthy those derived from species which differ exceedingly from one another in form and size. One cannot easily imagine two plants in the limits of a single genus which present a greater contrast to one another in respect of flowers, leaves, and general mode of growth than is exhibited in the following cases:—*Saxifraga cæsia* and *S. mutata*, *S. aizoon* and *S. cuneifolia*, *S. aizoides* and *S. squarrosa*, and yet hybrids have sprung from the crossing of these species.

About two hundred hybrids, for the most part fertile, have come into existence in nature within the family of the Rosaceæ. The genera *Geum*, *Potentilla*, *Rubus*, *Rosa*, and *Sorbus* are inexhaustible in the formation of hybrids. On the other hand, the Papilionaceæ, a family allied to the Rosaceæ, is peculiarly wanting in hybrids.

This discrepancy between nearly-related families in respect of the number of their hybrids is again noticeable in the class of plants known as the Monopetalæ. The Labiata, e.g. the genera *Ajuga*, *Prunella*, *Calamintha*, *Lamium*, *Marrubium*, *Mentha*, *Salvia*, and *Stachys* include numbers of hybrids, whilst the Boraginaceæ have very few. Of the latter only one or two hybrids are known, and these belong to the genera *Pulmonaria* and *Symphytum*. The Scrophulariaceæ and Rhinanthaceæ have long been noted for the great variety of their hybrids; the genera *Pedicularis* and *Verbascum* in particular exhibit a great wealth of forms, *Pedicularis* in alpine regions and *Verbascum* on the shores of the Mediterranean. *Verbascum* alone includes more than fifty. In the case of Gentianaceæ, also, the products of a great number of different crosses are found in the Alps, the chief parent-species being the long-stalked *Gentiana lutea*, *G. Pannonica*, *G. punctata*, and *G. purpurea*. Primulaceæ, whether growing on the upper or the lower levels of mountains, are famous for the abundance of their hybrids. In the genera *Androsace*, *Primula*, and *Soldanella* the number of hybrids identified by Botanists surpasses the number of the species from which they have sprung. The Ericaceæ, although comparatively poorly represented in Europe, exhibit several hybrids derived from the genera *Erica*, *Rhododendron*, and *Vaccinium*.

Hybrids are also specially numerous in the family of the Rubiaceæ, the genus *Galium* being the most prolific in this respect. But the greatest number of all is to be found amongst the Compositæ. More than two hundred hybrids have been identified in the genera *Achillea*, *Carduus*, *Centaurea*, *Cirsium*, *Hieracium*, *Inula*, and *Lappa* alone. Of hybrid Compositæ the following are particularly worthy of notice:—*Erigeron Hülsenii*, which is the result of a cross between *Erigeron Canadense*, an annual species brought into Europe from America, and *Erigeron acer*, a perennial species indigenous to Europe, and, secondly, the Cudweed hybrids, *Filago mixta*, *F. neglecta*, *F. subspicata*, &c., which spring from crosses between annual species, and are, therefore, exceptional, for annual species in general rarely produce hybrids.

In many cases only a few individual instances of these natural hybrids have been observed; in some, indeed, one single specimen alone has as yet been discovered. The majority, however, grow by the hundred or by the thousand in the localities proper to them, and many are represented by immense numbers of plants, and possess a wide area of distribution. *Salvia betonicifolia*, a hybrid derived from *Salvia nemorosa* and *S. nutans*, occurs as commonly as its progenitors in places on the grassland in the central parts of Siebenbürgen (Hungary); *Marrubium remotum*, a hybrid of *Marrubium peregrinum* and *M. vulgare*, is to be found everywhere on the plains of South-Eastern Europe, especially in the flat country by the Theiss and

the lower Danube: *Roripa anceps*, the hybrid of *Roripa amphibia* and *R. sylvestris*, is met with all over the district forming the basin of the Baltic; *Primula digenea*, a hybrid derived from *Primula vulgaris* and *P. elatior*, grows in its thousands in the upland meadows of the Eastern Alps; *Betula alpestris*, produced by the crossing of *Betula alba* and *B. nana*, is met with in great abundance in the Jura, in Scandinavia, and in the North of Russia, and here and there entire copses are composed of it; *Nigritella suaveolens*, a hybrid produced from *Gymnadenia conopsea* and *Nigritella nigra*, is so common in the Central Alps, for instance, in the Pusterthal of Tyrol, that hundreds of specimens are sometimes encountered in a single meadow; *Primula Salzburgensis*, the hybrid of *Primula glutinosa* and *P. minima*, is represented by a host of plants on the Tyrolese Alps, as, for instance, on the Muttenjoch and the neighbouring mountains which separate the Gschmitzthal from the Oberrnberghthal.

Several hundreds of other cases of the kind might be mentioned, but the limits of this book will not allow me to do more than give the following names selected from the long list that lies before me:

HYBRID.	PARENTS.
<i>Asplenium Germanicum</i>	<i>Asplenium Ruta-muraria</i> × <i>A. septentrionale</i> .
<i>Calamagrostis acutiflora</i>	<i>C. arundinacea</i> × <i>C. epigeios</i> .
<i>Carex Boëninghausiana</i>	<i>C. paniculata</i> × <i>C. remota</i> .
<i>Scirpus Duvalii</i>	<i>S. lacustris</i> × <i>S. Pollichii</i> .
<i>Juncus diffusus</i>	<i>J. effusus</i> × <i>J. glaucus</i> .
<i>Orchis Dietrichiana</i>	<i>O. tridentata</i> × <i>O. ustulata</i> .
<i>Potamogeton spathulatus</i>	<i>P. polygonifolius</i> × <i>P. rufescens</i> .
<i>Populus canescens</i>	<i>P. alba</i> × <i>P. tremula</i> .
<i>Salix Austriaca</i>	<i>S. grandifolia</i> × <i>S. purpurea</i> .
<i>Rumex maximus</i>	<i>R. aquaticus</i> × <i>R. Hydrolapathum</i> .
<i>Polygonum mite</i>	<i>P. Hydropiper</i> × <i>P. Persicaria</i> .
<i>Cistus Florentinus</i>	<i>C. monspeliensis</i> × <i>C. salvifolius</i> .
<i>Draba Hoppeana</i>	<i>D. Fladnizensis</i> × <i>D. Carinthiaca</i> .
<i>Roripa stenocarpa</i>	<i>R. palustris</i> × <i>R. sylvestris</i> .
<i>Pulsatilla Hakelii</i>	<i>P. patens</i> × <i>P. pratensis</i> .
<i>Drosera obovata</i>	<i>D. longifolia</i> × <i>D. rotundifolia</i> .
<i>Epilobium salicifolium</i>	<i>E. alsinifolium</i> × <i>E. montanum</i> .
<i>Sorbus latifolia</i>	<i>S. Aria</i> × <i>S. torminalis</i> .
<i>Potentilla procumbens</i>	<i>P. erecta</i> × <i>P. reptans</i> .
<i>Mentha nemorosa</i>	<i>M. aquatica</i> × <i>M. sylvestris</i> .
<i>Pedicularis atrorubens</i>	<i>P. incarnata</i> × <i>P. recutita</i> .
<i>Verbascum rubiginosum</i>	<i>V. Austriacum</i> × <i>V. phæniceum</i> .
<i>Acanthus spinulosus</i>	<i>A. mollis</i> × <i>A. spinosissimus</i> .
<i>Gentiana Charpentieri</i>	<i>G. lutea</i> × <i>G. punctata</i> .
<i>Primula pubescens</i>	<i>P. Auricula</i> × <i>P. hirsuta</i> .
<i>Vaccinium intermedium</i>	<i>V. Myrtillus</i> × <i>V. Vitis-idaea</i> .
<i>Erica Mackayi</i>	<i>E. ciliaris</i> × <i>E. Tetralix</i> .
<i>Cirsium tataricum</i>	<i>C. canum</i> × <i>C. oleraceum</i> .
<i>Lappa pubens</i>	<i>L. minor</i> × <i>L. tomentosa</i> .
<i>Hieracium stoloniflorum</i>	<i>H. aurantiacum</i> × <i>H. pilosellaforme</i> .

The fact that hybrids exhibit every conceivable degree of frequency of occurrence might lead one to suppose that the rare hybrids were those that had been most recently produced, and that they exist only as isolated plants because they have not

yet had time to disperse and multiply. This conception would not, however, accord with the actual condition of affairs. In point of fact, the floral contrivances which exist for promoting crosses between different species occasion a constant origination of hybrids, but it is certainly not the case that they all have the prospect of becoming new species. Many are called, but few are chosen. In only a fraction of the total number of fresh plant-forms produced yearly by inter-specific crosses do we find the power to survive and multiply. The first condition that must be fulfilled if a hybrid is to become a species is that it be fertile, *i.e.* that its flowers yield seeds capable of germination as a consequence of fertilization with their own pollen. By "their own pollen" is here meant not only that which is developed in the same flower as the stigma which receives it, or in some flower on the same plant, but also pollen belonging to other plants provided they belong to the same hybrid-formation. To this condition another is added in the case of diceious, pseudo-hermaphrodite, and completely dichogamous flowers, *viz.*: that several individuals of the hybrid must make their appearance at the same time, and that of these at least one must bear male flowers and one female flowers. If we suppose the case of a Willow hybrid, of which all the individual-plants bear catkins of male flowers only, obviously no propagation by means of fruits is possible. If none but female flowers are borne, these may be crossed with the parent-species and give rise to goneoelinic hybrids (*cf.* p. 559), and perhaps, in addition, ternary hybrids may be produced, but no unmodified descendants can be expected from the fruits of a Willow of the kind. The same thing applies in the case of *Cirsium*, the separate individuals of this genus being differentiated into those bearing pseudo-hermaphrodite male flowers and those bearing pseudo-hermaphrodite female flowers (*see* p. 294). This affords sufficient explanation of the fact that although Willows and *Cirsiums* are continually developing numberless hybrids, few instances are known which one can affirm to be the beginnings of new species. It usually happens, in fact, in the case of these hybrids, that all the plants which arise together at a particular spot are furnished exclusively either with true or pseudo-hermaphrodite male flowers, or else with true or pseudo-hermaphrodite female flowers. The goneoelinic hybrids produced from the latter are for the most part represented by greater numbers of individuals. Moreover, amongst those individuals both sexes much more frequently make their appearance: hence, they have a far better prospect of being preserved.

The development of a hybrid into a species is also dependent on the conditions determined by the habitat. When a species thrives well at a particular place, is represented by a large number of individual plants, and renews itself in descendants which are in the main unchanged, it may be assumed that the organization of that species is suited to the soil and climate of the habitat in question. If there were no such harmonious relation there could be no question of the species flourishing, but on the contrary it would sooner or later die out. This suitability of the climate and soil to the organization manifested in the plant's external form must also exist in the case of the newly developed hybrid if the few individuals which spring up at any particular place are to survive in their original settlements, and to give rise to

a numerous progeny. Sometimes such suitability does exist, but sometimes also it does not. In the latter case the hybrid is suppressed as soon as it sees the light. But even if its organization is adapted to the soil and climate of the place of origin, it has to enter upon a struggle with the species already established there, and especially with its own parent-species. If the latter grow luxuriantly and in large numbers at the spot, it is not easy for the new form to take possession of the ground. In two cases only is there any prospect of the place of origin becoming a permanent home for the hybrid's descendants: firstly, where the hybrid, in virtue of its particular attributes, is equally well, or perhaps even better adapted to the habitat of the parent-species than are the plants already established there, and secondly, when the hybrid originates at a spot more or less removed from the place where the parent-species grow and encounters conditions of soil and climate which agree with it better than with the parent-species.

That these conditions of the origin of species from hybrids are sometimes fulfilled will now be shown by a few examples. In the Tyrolese Alps, to the south of Innsbruck, at the head of the valleys known as the Stubai thal and the Gschnitz thal, there are certain mountains which rise steeply to a height of from 2500 to 3000 metres. The base of these mountains is composed of crystalline schist; midway up their ascent mixed strata of schist and limestone are encountered; and above these strata there is limestone and also dolomite, rising abruptly and forming the peaks and ridges. Half-way up the sides, where the soil exhibits great variety, an extraordinarily rich flora is developed. Plants which are, except in this instance, peculiar to schist formations, and others usually only found on limestone, here grow close together. Amongst other species the Alpine Roses, *Rhododendron ferrugineum* and *R. hirsutum*, grow side by side on the same soil and on the same slopes. Associated with them is a third species of Alpine Rose, *Rhododendron intermedium*, which has sprung from the crossing of *R. ferrugineum* and *R. hirsutum*. At several places, e.g. on the eastern and northern slopes of the Hohe Burgstall, in the Stubai thal, and on the Padaster Alp in the Gschnitz thal, *Rhododendron intermedium* occurs more commonly than either of the parent-species. Like the latter, it grows on soil rich in humus, flowers abundantly, develops fruits with fertile seeds, and transmits its characteristics unaltered to its descendants. Here and there isolated plants are found which must be ranked as goneoclinic hybrids, but plants of *Rhododendron intermedium* form the larger proportion of the Alpine Roses which clothe the mountain-sides. This form accords in every particular with the requirements demanded of a species, and is quite as much a systematic entity as either *R. ferrugineum* or *R. hirsutum*. The following is the explanation of how this has come to pass: The colour of the flowers is a little lighter than in *R. ferrugineum* and richer than in *R. hirsutum*; it is a brilliant carmine tint, and enables one even at a distance to identify every plant of the hybrid. Hive- and bumble-bees hovering about in search of honey are more attracted by flowers of *R. intermedium* than by the others, owing to the superior brilliancy of their coloration, and the result is that these flowers are

crossed with pollen of their own kind. If no insects appear upon the scene, autogamy takes place. In either case fertile seeds are developed, and give rise to plants which do not differ from the parent-form. In places where detritus from the adjacent limestone and dolomitic cliffs is mixed with the humus of the soil the seedlings thrive distinctly better than those of *R. ferrugineum* and no less well than those of *R. hirsutum*. Thus, so far as the soil is concerned, *R. intermedium* has an advantage over *R. ferrugineum*, and in respect of insect-visits it is better off than either of the parent-species. These advantages, though apparently insignificant, are not merely sufficient to prevent *R. intermedium* from yielding to the parent-species in the struggle for existence at the places in question, but even give it rather a better chance of prevailing.

As a second instance, we will take *Salvia sylvestris*, the hybrid offspring of *Salvia nemorosa* and *Salvia pratensis*. This plant grows in dry meadows all over the low country to the south of Vienna, as, for instance, on the banks of the river Leitha, which separates Austria proper from Hungary. The landscape there is slightly undulating, the elevations are composed of boulders and clay, and wherever the latter is present in great quantities, especially on the gentle slopes of the rising ground, *Salvia nemorosa* constitutes an important item in the vegetation. The hollows are full of a dark moist earth, with a rich admixture of humus, and there we find meadows in which *Salvia pratensis* grows luxuriantly. These two kinds of habitat usually pass quite gradually into one another, and the parts common to both consist of dry meadow-lands. *Salvia nemorosa* does not thrive in the intricate grass-carpet of these meadows, and is rarely to be seen there, whilst for *Salvia pratensis* the soil is too dry, so that that species also is but poorly represented on the areas in question. On the other hand, these dry meadows are the most suitable ground for the hybrid *Salvia sylvestris*, and it thrives exceedingly upon them. Its flowers are much visited by insects; its fruits ripen in as large numbers as in the case of *S. nemorosa* or *S. pratensis*, and have been found by experiment to be fertile in a proportion of more than 60 per cent. *Salvia sylvestris* has therefore scattered itself all over this dry meadow-land, and manifests all the characteristics essential to our conception of a species.

A third example is *Nuphar intermedium*, a hybrid derived from *Nuphar luteum* and *Nuphar pumilum*. This plant grows in lakes in the Black Forest and in the Vosges. It is also scattered over North Germany, and occurs with increasing frequency in Central and Northern Russia and in Sweden. It has been found as far north as Lapland. At the northern extremity of this large area of distribution *Nuphar intermedium* is more abundant than the species from which it is derived; indeed in many places it occurs in their absence, and in fact passes beyond the northern limits of their area of distribution. In these situations there is, of course, no possibility of the hybrid's crossing with either of the parent-species or of the formation of goneoclinic hybrids. *Nuphar intermedium* subsists independently there, multiplies without change of form, and has in fact established itself as a species. This phenomenon is explained as follows: The northern limit of

the distribution of each of the three Water-lilies in question is determined by their not being able to ripen fruits beyond that limit. Of the three, *Nuphar luteum* flowers the latest, and therefore its fruits are also the latest to ripen, whence it follows that it is the first to fall behind; that is to say, it reaches the northern limit of distribution sooner than the others, and ceases to ripen fruit in regions where the others are still able to do so. But *Nuphar pumilum* and *N. intermedium* are also different from one another in this respect. In Norbotten and Lapland *Nuphar intermedium* ripens its fruits a little earlier than *N. pumilum*, and it is consequently able to extend rather further north than *N. pumilum*. The further north plants go, the shorter becomes the time allotted for the performance of their annual work; and those which ripen their fruits early have a great advantage over those which ripen later. Concerning *Nuphar intermedium*, it has also been ascertained that the individual plants produced in nature are more fruitful than those reared in gardens from artificial crosses. In the case of plants obtained in this manner in the Botanic Gardens at Königsberg each capsule contained from 15 to 18 fertile seeds, whilst capsules ripened in the small lakes of the Black Forest contained from 38 to 63, and others taken from plants growing in Lapland contained from 41 to 72 such seeds. From these data we may infer, in the first place, that *N. intermedium* is most prolific in situations beyond the range of the parent-species; and, secondly, that it would be wrong to suppose that because a hybrid may be comparatively infertile or actually sterile in a particular locality, such infertility is a characteristic of the plant wherever it may occur.

As may be gathered from the above account of these three examples, the advantage which a hybrid may possess over the parent-species, whereby it is enabled to subsist and multiply side by side with those species, is not always of the same kind. In one case it is the more vivid coloration of the flowers, in another the fact of the hybrid being better adapted to a particular state of the ground, whilst in the third the earlier ripening of the fruits, which enables the hybrid to stand a more rigorous climate, gives the requisite advantage. These do not, of course, exhaust, by a long way, the possible sources of superiority, and there are many instances of hybrids which thrive better than the parent-species when the climate becomes milder, moister, or drier, as the case may be. It is obvious that of all the different advantages which may come into play those connected with climatic conditions are the most important, and the genesis of hybrids is probably most frequently due to the operation of this kind of advantage.

Far too little significance has been attached to the fact that the greater number of hybrids are not found in districts where the parent-species grow together with equal luxuriance, but occur where one or other of those species is meagrely represented, owing to the climate not being favourable to its distribution. Again, large numbers of hybrids are found in parts where the boundaries of several species coincide. In Europe such regions exist in the strips of land where the advance-posts of the Floras of the Baltic and Black Sea, and the Floras of the Baltic and the Mediterranean, respectively, encounter one another, and particularly in the

lower limits of the Alpine Flora. Another characteristic of these borderlands is the fact that the separate hybrids growing on them are almost always represented by a large number of individuals, and the consequence is that there is no great chance of their crossing with the parent-species and gradually reverting, in successive generations, to those species. If isolated individuals belonging to a particular hybrid grow in the midst of thousands of plants of the parent-stocks, their stigmas will, in all probability, be dusted with pollen from the latter species. This probability diminishes, however, as the number of individuals of the parent-species flowering in the same locality as the hybrid diminishes; if that number is small the hybrid is thrown mainly upon its own resources for fertilization, and, provided it is self-fertile, there is nothing to prevent its multiplying and becoming dispersed.

Connected with the above is the further fact that in the neighbourhood of a hybrid which has become a species there is sometimes no trace of one of the parent-species, it having completely died out. The slightest change in climatic conditions may cause the plants of a particular stock to succumb at the confines of the stock's area of distribution, where they are only present in small numbers, and are anything but strong; and when this happens we find the other parent-species alone growing side by side with the hybrid, and even that species is possibly not so well adapted as the hybrid to the altered conditions. Of cases in point we will select two from the East of Europe and two from the West.

When *Epilobium alsinifolium* and *Epilobium palustre* are crossed a hybrid is obtained which, when fertilized with its own pollen, yields a large quantity of fertile seeds. The plants reared from these seeds exhibit the same characteristics as the plant from which the seeds were taken. This hybrid grows together with the parent-species in the Riesengebirge, and has received the name of *Epilobium scaturiginum*. It is likewise a native of the Bihar Gebirge, on the confines of Hungary and Transylvania, and is of very common occurrence in the springs and rivulets in the vicinity of the Hoehkamm (a mountain of this chain). Yet, of the two parent-species, only one, viz. *Epilobium palustre*, grows amongst these mountains. Again, *Prunella hybrida* is a hybrid springing from *Prunella laciniata* and *Prunella vulgaris*. It is widely distributed in the Wienerwald district, and in some places is commoner than the parent-species, whilst in Moravia and Bohemia it occurs in places where one of the latter, viz. *Prunella laciniata*, is entirely absent. A third instance is afforded by *Primula brevistyla*, called also *Primula variabilis*, a hybrid derived from *Primula vulgaris* and *P. officinalis*. This plant is true to seed, and is met with everywhere throughout almost the whole of Europe in company with both parent-species. In some districts of France it is found also in places where one or other of the latter species does not grow at all, and even where both are absent. Our fourth example, *Linaria stricta*, is the hybrid of *Linaria striata* and *Linaria vulgaris*. It occurs in many places in the West of Europe, together with its progenitors, but in the South of France, in the neighbourhood of Montpellier, it is found growing with *Linaria striata* alone, whilst the other parent-stock, *L. vulgaris*, is never found in the district.

We shall have another opportunity of describing the way in which the lines of demarcation of the ranges of entire floras become displaced in consequence of the changes which the climate of a region is liable to undergo in course of time. These displacements of floral regions are, as a rule, the result of very slow and inconspicuous migrations on the part of the plants constituting the floras in question. The direction of migration is invariably towards the places whose climatic conditions agree best with the organization of the plants, and is, in the case of any one species, either an advance or a retreat, according to the nature of the circumstances which impel the species to migrate. The different plants of a flora do not all migrate in a host together. Some species abandon their former home entirely and establish themselves in a new locality more or less remote from it; others leave a few of their kind behind in the old settlement at isolated spots which happen to be in peculiarly favourable situations, and many succumb to the effects of the new conditions or to the hardships incidental to the migration, and so die out. These changes in the range of floras are naturally accompanied by all sorts of alterations in the social relationships of the plants concerned especially with regard to the co-existence of hybrids and their progenitors. It may happen that one or both parent-species are left behind, whilst the hybrid advances, or the hybrid may remain behind, whilst one of the parent-species advances; or, again, one of the parent-stocks or both may die out. The facts concerning these local displacements explain the phenomenon that species which, from their characteristics, may be looked upon as hybrids of two other species, occupy in each case a district which is separated, and often at a considerable distance, from the areas inhabited by the species supposed to be their progenitors. The characteristics of the kind of Sorrel named *Rumex Patientia* lead one to the conclusion that it is a hybrid derived from *Rumex aquaticus* and *Rumex crispus*. It is found, however, growing wild in Hungary and in Bosnia in parts where neither *Rumex aquaticus* nor *R. crispus* occurs at all. In Herzegovina there grows fairly commonly a *Micromeria* which has been named by one of my friends *Micromeria Kernerii*. So far as its characteristics are concerned it must be considered to be a hybrid of *Micromeria græca* and *Micromeria Juliana*; yet neither of these two species grows in Herzegovina at the present time, and they are not met with at any nearer spot than the part of Dalmatia which stretches westward from Herzegovina, and belongs to the area of distribution of the Mediterranean flora. In the little upland valleys of Planail and Plawen, which run down from the mountains of the Oetzthal into the valley of the Adige, there grows a *Pulsatilla* named *Pulsatilla nutans*. If it occurred in company with *Pulsatilla vulgaris* and *Pulsatilla montana*, all Botanists would be unanimous in looking upon it as the product of a cross between those two species. Yet *Pulsatilla vulgaris* and *P. montana* do not grow in the high valleys in question, but are first met with at a distance of many miles from them, the former in the Unterinnthal and the latter in the Vintschgau (a portion of the Adige valley).

Inasmuch as the last-mentioned cases have to do with processes which have taken place long ago they partly belong to the next chapter, where the genesis of

species in the past will be discussed. They here bring to a natural conclusion a series of examples adduced to show in what manner a genesis of new species may ensue in the present, and may have taken place in the past. No sharp line of demarcation is to be found between different epochs in this connection any more than in the case of any of the other phenomena which, in the aggregate, constitute the history of species.

Now that it has been shown how new species arise from hybrids, or, in other words, from the crossing of species in pairs, the question presents itself whether, in addition to this one method, there are not also others leading to the same result. In answering this question we must bear in mind that every permanent change in external form which is inherited by a plant's descendants must be preceded by a change in the constitution of the protoplasm, and that so far as investigation has elicited the facts, the centre of the change is located exclusively in a particular protoplast which lies hidden in the ovary and there receives the spermatoplasm. The stimulus which causes the change in this protoplast can only proceed from the spermatoplasm, and every speculation concerning the formation of new species must therefore be associated with the question whether in the intercrossing of plants of one species and in autogamy the protoplasm in the course of its journey to the ooplasm may, as a result of its exposure to new external conditions, undergo modifications of so fundamental a kind that its influence on the ooplasm is subject to corresponding variations. In the first place, it might be imagined that the pollinated stigmas do not always act in the same way upon the spermatoplasm of the pollen-cell. Reference has already been made to the fact that a stigma may sometimes be almost simultaneously dusted with the pollen of very different plants (see p. 404), but that it has the power of exercising a selection, and that in every case only one kind of pollen is induced to put forth tubes by which a real fertilization is accomplished. The other kinds of pollen upon the stigma are not known to have a direct effect upon the ovule. But that there is some interaction between them and the protoplasm in the cells of the stigma is evidenced by the fact that they swell up wherever they are in contact, and (as has been shown, p. 414) are frequently found developing pollen-tubes. Now it is possible that the reciprocal action of the contents of these pollen-cells and the contents of the stigmatic cells may produce some change in the latter, which is transmitted to the contents of those other pollen-tubes which are to enter into combination with the ooplasm. Such modification might conceivably affect the nature of the stimulus imparted to the ooplasm, and this alteration in the stimulus might be manifested in a change in the form of the individual arising from the fertilized ooplasm. The likelihood of all these possibilities and assumptions being satisfied is extremely small, but as no researches have yet been instituted into the matter, it cannot be dismissed with an unconditional negative.

In artificial crosses between different species of *Cirsium* it has often been noticed that pollen-cells taken from a single capitulum vary in their effects upon the stigmas of a second capitulum, inasmuch as the seeds produced by the different florets, though all fertilized with the same kind of pollen, yield dissimilar plants when

they germinate. The variation is limited, it is true, to the different degrees in which the seedlings resemble one or other of the parent-plants. If the cross is between two plants of the same species no such variation can occur, seeing that the plants crossed are alike in form. But there is still the question whether differences in the age, size, and luxuriance of growth of the individuals which cross may not have some influence on the result. So far as my experiments show, these differences have no effect on the genesis of new forms, and have no prospect of becoming permanent characters in the offspring. A poor stunted plant growing on dry soil may produce seeds which, on being planted in a good moist soil give rise, under favourable conditions, to well-developed plants capable of flowering luxuriantly. As is well known, the first flowers of an inflorescence are always much larger than those which subsequently open at the apices of the spike or raceme, or on the ultimate ramifications of the cyme as the case may be. Now, if the large earliest flowers are crossed one with another, and likewise the small latest flowers, and the seeds so obtained in each case are kept separate but reared under similar conditions, the plants produced from them do not differ in the slightest degree from one another, but in their turn bear flowers, of which the first are the largest and the last the smallest. Notwithstanding these results, however, I should not like, without further investigation, to deny the possibility of the specific constitution of the spermatoplasm undergoing some change as a result of external influences in the course of its development, whether during its imprisonment in anthers or antheridia or on its way to the ooplasm, or to say such change might not cause the descendants of the plants concerned to differ in form from the individual from which they sprang.

It has been established beyond all doubt that modifications of form directly induced by conditions of soil or climate are not hereditary, and that every change of form which persists in the descendants is only brought about as the result of a process of fertilization, or, in other words, that new species can only arise through fertilization. Herein lies also the solution of the marvellous phenomenon known as the alternation of generations, and of the question why plants in general flower and undergo fertilization. To these processes is due the genesis of new species. The propagation of plants, their multiplication and dispersal, may also be effected by means of brood-bodies, and as a matter of fact these processes are continuously operating on a vast scale. But the plants reproduced by brood-bodies retain the form of their ancestors unaltered, and no new forms arise in this way. Suppose that a locality is occupied exclusively by plants which multiply by brood-bodies only and do not change their form, and that in consequence of a change in the climate such species as are not adapted to the new conditions abandon their homes, or else languish and die out, the probability is that many of the vacated spots will remain unoccupied owing to there being no recruits in the neighbourhood, or from out its confines, that are better adapted to the new conditions. If, on the other hand, the area in question is inhabited by plants which reproduce sexually and which, by crossing one with another, produce descendants of diverse forms, there is

every probability that amongst the assemblage of new forms some will be better adapted to the new conditions when a change of climate occurs than those of the old species which are driven out thereby, and that these new forms will therefore be able to take the place of the latter.

It is only from this standpoint that we can properly understand the phenomena of the alternation of generations, the separation of the sexes, dichogamy, and all the rest of the wonderful floral contrivances, the object of which is to facilitate the crossing of two species during the first stage of flowering and only to allow of crossing between plants of one species, or of geitonogamy, autogamy, or cleistogamy in the event of no inter-specific crossing taking place. As a result of these contrivances, numberless new forms are continually being generated which are respectively adapted to all the most various conditions of soil and climate. So long as no change in climatic conditions takes place, the majority of these forms have very little chance of surviving and of naturalizing themselves as species amongst the plants already established in the same locality. But when, in consequence of a change of climate, the ranks of the species in possession of the ground are thinned through the abdication of many of those best adapted to the conditions of life previously existing, the real significance of the new forms which have arisen as a result of the sexual process is manifested in the fact of those which are best adapted to the new conditions taking possession of the spots vacated and settling down there as new species.

DERIVATION OF EXISTING SPECIES.

The plants preserved as fossils in former ages are not only the forerunners but the ancestors of the existing vegetation of to-day. There was no general rejuvenescence and extinction of organisms coincident with the beginning and end of the several "periods" of the history of the earth. The changes in the organic world, like those in the inorganic crust of the earth, were accomplished gradually by slow degrees, and the organisms of the present day are a continuation of, and have been slowly evolved from, those of former ages.

So far, there is little difference of opinion amongst naturalists; but as to the causes of the differences in form between the vegetation of the present and the past, the most various theories are held. Nor is this surprising, seeing how largely our conclusions are based on conjectures. And when the flood-gates of speculation are rolled back it is not always that the proven is clearly distinguished from the unproven. An import is attached to isolated facts which they do not merit, and—most mischievous of all—the existence of wide lacunæ in our knowledge is concealed, or these lacunæ are dexterously bridged over with unmeaning, high-sounding words and hollow phrases which, while astonishing us for the moment, leave us chastened and confounded. The confirmed mistrust aroused by these extravagances which obtains concerning all that bears on the derivation of species demands that we should devote a brief consideration to the prevailing theories, and especially to

such as bear upon the conversion of species of former times into those of the existing vegetation.

A change in the conditions of life has, according to a widely-spread view, been the immediate cause of a change in the vegetation. The altered conditions of life provoke new wants in the plant, and these new requirements have led to a transformation of their organs. Stimulated by use, the organs in question become enlarged and further developed; others, no longer of service, become smaller, atrophy, and disappear. It is the cumulative result of these small and almost imperceptible changes that in course of time becomes apparent. These structural changes are transmitted to the progeny, and with an increasing tenacity, the greater the number of generations which have been exposed to the altered conditions. This, the *theory of adaptations*, has provoked wide discussion and criticism. It is urged against it that, whether wild or cultivated plants be considered, it is only isolated or a few individuals, never the whole of the members of a species, which exhibit these variations and transmit them to their offspring. If these new characters are immediately due to the soil or climate, then all the individuals of a species, exposed to like conditions of growth (environment), should exhibit them and hand them on to their offspring. The permanence of the influence—and to this many naturalists and others attach great importance—is without significance in this matter. When a change is called forth—be it by an altered source of nourishment, by the influence of heat or cold, light or darkness, moisture or dryness—it must become apparent upon the growing plant, since a change in the plant stands to a change in the environment as effect to cause. If the cause ceases, so also does the effect, equally after the lapse of a year or a hundred years. But a much more potent criticism of the theory of adaptation is the result of a series of experiments which were carried out for the solution of these questions. From them we see that an altered environment calls forth certain changes in the plants submitted to it, but that these are not transmitted to the offspring, are not hereditary, and that the influences of soil and climate do not provoke a fundamental change in the constitution of the protoplasm. Influences of this sort can induce a diseased condition in a plant and can even kill it, but they cannot bring about a change which can be transmitted to the next generation. Though soil and climate play a most important part in the struggle of species and varieties for existence, and though the environment has a great influence on the origin of varieties and on the distribution and migration of plants—as the immediate stimulus to the origin of new and transmissible characters, and thus to the modification of species, change of environment is without significance.

Another theory dealing with the origin and modification of species is that known as the *theory of progressive transformation by inherent forces*. According to it, the impulse to change resides in the inherent tendency of all species to perfect themselves. This theory transcends all experience and depends on premises and draws conclusions essentially metaphysical in nature; it deals only in part with the results of scientific observation. It presupposes a creation of living

protoplasts endowed with the capacity to alter their constitution on their own initiative; and, further, that these alterations take place along predetermined lines in a direction leading from a lower to a higher platform; consequently the imperfect organism necessarily, in course of time, passes over into a highly developed, perfect one. Against this theory the following may be urged: The first assumption involves creation. The question is: Is it possible for a living protoplast to be formed from inorganic matter without the co-operation of already existing living beings? The question obviously concerns the present and future as well as the past, for what has happened once may again take place, for the forces of nature, according to the laws of the conservation of matter and energy, remain the same for all time. The discussion of this question resolves itself into this: whether a little bit of protoplasm can arise from inorganic matter, and after its origin can acquire the capacity of growing by the absorption of food from its environment, &c.: in a word, whether it can exhibit those changes and movements which we term life. When first organic compounds (formic acid, urea, sugar, &c.) were synthesized in chemical laboratories from inorganic substances like ammonia, carbonic acid, and water—compounds which formerly had only been produced as a result of the activity of living protoplasm—naturalists began to think that these things might take place in nature independent of already existing plants. It seemed possible that these substances might, under the uncontrolled forces of nature, unite and arrange themselves in the same manner as occurs within a vegetable cell. The tendency of matter to combine, which plays so important a part in nature, was pointed out, and especially the similarity between the structure of crystals and that of certain cells; the properties of finely-divided soil also were called to mind, how it absorbed gases, took up water in varying quantities, altered salt-solutions, separating certain of their constituents, and what was especially noteworthy, increased the capacity of many simple substances to combine. This was at a time when chief importance was attached to the chemical properties of protoplasm; it was thought that, once given the substance, it would form itself into cells like crystals. Of the ultimate structure of protoplasm and of the nucleus knowledge was as yet very incomplete. The tendency of that time was to explain all those phenomena which constitute life as the resultant of the various forces which form inorganic bodies, and to deny the existence of any wide gulf between the living and non-living world.

The experiments to produce living matter had all of them negative results. But this of course is no proof of its impossibility; for it can always be urged that wrong methods were followed, and improper conditions imposed. Nor, on the other hand, does it follow from the fact that hitherto living matter has never been known to originate independently of existing organisms, that its production is impossible. Since we cannot arrive at definite results by experiment, the investigator must depend on other considerations.

The second assumption of the theory of transformation from internal causes, that plants have the inherent capacity to modify their internal constitution and,

similarly, their external form spontaneously, has been so fully met by the observations recorded in the last chapter that it is hardly necessary to deal with it now at great length. I shall content myself with pointing out that it is impossible to give a natural explanation of such a phenomenon. Every variation presupposes a corresponding disturbance: for the acquirement of any new structural character the plan of construction must undergo some fundamental alteration. The naturalist is unable to grapple with the phrases "internal causes", "internal force", "force of transformation", "tendency to differentiate", "principle of progressive transformation", when attempting to explain variation in a natural manner upon mechanical principles. Nor is the likening of this transformation to the metamorphosis which every individual passes through at various periods of its existence at all to the point, since metamorphosis repeats itself with great constancy in every species according to the plan of construction which is laid down in the specific constitution of the protoplasm. That the protoplasm of any species should, in the absence of any impulse or stimulus from outside, be able spontaneously to alter its plan of construction contradicts all our experience of the normal action of natural forces. Even should we conceive vital force, the dormant energy of the protoplasm, to be converted into an active form, it could only give rise to movements which have their origin in the specific constitution of the protoplasm.

And now we come to the assumption that this inherent force of transformation is a progressive one, that it leads to a higher or more perfect development. But what is to be regarded as a higher development amongst plants? A tree with its brightly coloured flowers and luscious fruits seems more highly developed to the non-botanist than a low herb with inconspicuous flowers, or than the green filaments of a *Spirogyra* destitute of flowers. The supporters of the theory under discussion assert that the highest development is that which exhibits the greatest complexity of form, and in which division of labour is carried furthest. And in this assertion they do not essentially differ from the popular view. Complexity of form and division of labour are undoubtedly carried further in an Apple-tree than in the *Spirogyra* of the ponds and ditches. But it must not be forgotten that the differentiation of a plant-body into various tissues, the production of wood, bast, and cork in its stem, of cuticle, stomates, and hairs on its leaves, of various colouring-matters and aromatic substances in its petals, and of sweet juices in its fruits, stands in harmonious relation to the environment of the plant in question. Change the conditions, and imagine the Apple-tree submerged in a pond: it is no longer in harmony with its surroundings, its complexity of tissues, its wood, stomates, &c., are not so well adapted for these conditions as are the *Spirogyras* and Water-weeds equipped with organs of another type. The size of a plant is often—in the popular estimate—the indication of its high organization. A big plant gives the impression of possessing a more perfect development than a small one. But this criterion leads to no satisfactory result; it is sufficient to instance the case of certain huge sea-weeds (*Macrocystis*) of the southern seas, which exceed our greatest forest trees in height. Many Thallophytes, only visible under

the microscope, show a greater complexity of structure of their constituent cells than do many Flowering Plants: and, should especial importance be attached to this character, Diatoms and Desmids must be regarded as more highly organized than many small annual Composites. The idea of progressive development implies a recognition of that species of plant which is most highly developed and which stands upon the apex of the pyramid, or, at any rate, of the group of plants which has already reached the furthest point—is it the Aristolochiaceæ, Cannaceæ, Magnoliaceæ, the Orchids, the Composites, the Ranunculaceæ, the Papilionaceæ, or the Pomegranates? Any one who has studied carefully the structure of these plants knows well that it is impossible to make an estimate of this kind. In a book of Botany one group must be treated first and another last, but this does not necessarily imply that the last is the most highly developed; indeed the various writers of systematic works begin and end with the most various groups. Like the theory of adaptability, that of progressive transformations from inherent forces fails to give us a reasonable explanation of the variations which plants have undergone in process of time.

A third theory, based on the observations of modern times, is as follows: That variations of form in the offspring arise through crossing, from the union of two dissimilar protoplasts. This theory, based on the union of unlike forms, has been fully sketched out in the last chapter. It assumes the existence in former times of a vegetation rich in forms—an assumption amply justified by the fossil remains which have been preserved. New forms arose, not by a progressive development such as has been alluded to, but by a transformation or metamorphosis of those already in existence. It was from the union of existent types that incipient new species were produced. By the periodic recurrence of changes in climatic conditions the areas of plant-distribution have received continual displacements, and it was then that these incipient species or varieties were put to the test. Those well-suited to the fresh conditions settled down into new species. They replaced their less well-adapted ancestors in the plant-community, and they played the same part as these had formerly done. A change indeed is brought about; but not (on the lines of the theory of adaptability) as a direct result of climatic influences, nor from an inherent tendency to progressive development. It arises rather from a change in the specific constitution of the protoplasm in consequence of the crossing of unlike forms. In basing the transformation of species on a crossing of this nature we are relieved the necessity of picturing lacunæ in a vegetation as a result of climatic changes, or of any serious disturbance of the inter-relations of its various component forms. Bacteria and Moulds, Mosses and Liebens, Ferns, Grasses, Palms, and Coniferous Trees, have all of them a special function to fulfil in the great community of plants, and they are to a certain degree dependent on one another. Were one removed the whole would be affected, and it might well happen, did a given group come to speedy extinction, that the whole community of plants might suffer. But in every group at all times and in all places a reserve of new forms continually arises by crossing, so that this danger is averted. With climatic

changes, of the older, less fit forms some are extinguished, whilst young, new forms step into their places. Thus we see also that the conversion of Mosses into Ferns, of Ferns into Conifers, and of Grasses into Pinks, &c., as assumed by the theory of progressive transformation, would be a positive disadvantage to plants as a community, and that its tendency would be in the direction of anything but real progress.

It is important to recognize the fact that in the production of new forms by crossing, it is not especially such forms as are constituted to resist an anticipated change of climate that are produced. Of the forms which arise, some are fitted for a more inhospitable, others for a milder climate; but it cannot be said of any that they possess an assured future. Such only are able to maintain, propagate, and establish themselves, as are from their internal organization and external form in harmony with the prevailing climatic conditions of the moment. Those so constituted that they are unable to thrive under the given external conditions linger and become extinct: they are outstripped and overgrown by such as find the environment to their liking. Hence we speak of the struggle for existence. Plants in harmony with their surroundings are the victors, and they establish themselves upon the arena of this encounter. This, briefly, is Darwin's theory of Natural Selection, a theory which marks an advance upon all other theories of the origin of new species. Though many views may be held as to the precise manner of origin and transformation of forms, there can be no difference of opinion as to the significance of the struggle for existence and of the survival in this struggle of those forms best fitted by their organization to the circumstances of the environment.

THE SUBDIVISIONS OF THE VEGETABLE KINGDOM.

The fact that the savants of ancient times made no attempt to classify plants according to their structural characters is explained by their limited botanical knowledge. Their interest was restricted to such plants as were in use as drugs, poisons, and charms, to vegetables, fruits, and cereals, finally, to such as were of value for decorative purposes and as symbols of religious observances. Nor was the number of these plants considerable. Some five hundred forms were known to Theophrastus (300 B.C.), whilst Pliny (23-79 A.D.) records about twice that number. The characters of these few plants could be retained in the memory for the purposes of comparative investigations, and their recognition depended in large part upon the general impression gained in the ordinary intercourse with nature. Enumerations of plants were based far more on their medicinal or economic uses, on their hurtfulness and beneficence for mankind, than on any structural characters they might possess in common. Even in the herbals of the sixteenth century, containing, as they did, new descriptions and incomparable woodcuts, were the medicinal and economic properties of the various plants still especially emphasized: Botany was still almost exclusively the handmaiden of medicine and agriculture.

The first botanical writer to break with these old traditions was Clusius (1526-1609); he described plants as he observed them, quite apart from their value to man. Clusius, though a Belgian, spent many years of his life at Vienna, and thoroughly explored the Flora of Austro-Hungary; previously he had investigated the plants of Spain and Portugal. To England he paid more than one visit, and received many exotic plants from Sir Francis Drake, the voyager. In his *Rariorum Plantarum Historia*, published originally in 1576, we find the first attempt to classify plants according to their similar characters. In separate books he deals with trees, shrubs, and under-shrubs, bulbous plants, sweet-smelling flowers, scentless flowers, poisonous, narcotic, and acrid plants, with plants having a milky juice, and with Umbellifers, Ferns, Grasses, Leguminosæ, and certain Cryptogamic plants. In those days some 4000 plants were distinguished by Botanists, and the want of some system of classification was gradually felt. The groups of Clusius and his contemporaries were inadequate, and the system of Cesalpino (1519-1603), published in the first book of his *De Plantis Libri XVI* (1583), failed to obtain the recognition it undoubtedly deserved—perhaps because it was only sketched out in outline and lacked a full and detailed rendering. Cesalpino was the first to convert observation into real scientific research; he drew attention to the more hidden organs of plants, to the position of the seeds, the number and mode of insertion of the cotyledons, &c., to the presence or absence of flowers.

It is to Tournefort (1656-1708), a Frenchman, that we owe the first complete review of known plants in synoptical form. In his *Institutiones Rei Herbariæ* (published 1700) 10,146 species of plants are distinguished and arranged in 698 genera, which again are assembled under 22 classes. Classes 1-15 include herbs and under-shrubs, 16 and 17 flowerless plants (Cryptogams), and 18-22 shrubs and trees. The herbs, shrubs, and trees are distinguished by the form of their flowers, especial importance being attached to the presence of calyx and corolla, to the regularity or irregularity of the flower, and to the petals—whether they are free or united with one another. Not long afterwards Linnæus produced a classification of plants based on the distribution of the sexes, and especially upon the number of the stamens in the flowers. The terms species and variety, genus and class, were more clearly and intelligibly defined than heretofore, and his 1050 genera were included under the 24 classes already enumerated (p. 288). The Linnean classification, known as the Sexual System, enjoyed an unprecedented recognition. It constituted a well-arranged summary of a great mass of scattered observations, and made it possible for species to be identified by means of concise descriptions. It was not the fault of this accomplished and renowned naturalist if a greater importance were attached to his system than he himself ever intended. Linnæus never regarded these 24 classes as real and natural branches of the vegetable kingdom, and expressly says so: it was constructed for convenience of reference and identification of species. A real natural system, founded on the true affinities of plants as indicated by their structural characters, he regarded

as the highest aim of botanical endeavour. He never completed a natural system, leaving only a fragment (published 1738).

The credit of actually founding a natural system of plants is usually attributed to Bernard de Jussieu (1699-1777) and his nephew Antoine Laurent de Jussieu (1748-1836). For many years this system only found expression in the laying out of the beds in the Botanic Garden of Trianon (at Versailles); it first became generally known some thirty years after its inception, when the younger de Jussieu published his *Genera Plantarum* (1789). A hundred families of plants are distinguished and grouped under fifteen classes, which, in their turn, fall under three main co-ordinated divisions (Acotyledones, Monocotyledones, Dicotyledones). The three main divisions¹ are founded upon the structure of the embryo at germination. In the Acotyledones the embryo consists of but a single cell and is destitute of cotyledons, in the Monocotyledones it is multicellular and provided with one cotyledon, whilst in Dicotyledones there are two cotyledons. The Acotyledones are equivalent to the Cryptogamia of Linnaeus (his 24th class, cf. p. 290) and constitute the 1st class of the new system. The Monocotyledones fall into three classes according to the relative position of the stamens to the ovary (Monohypogynæ, Monoperigynæ, Monoepigynæ). The Dicotyledones are first subdivided into three groups according to the structure of the perianth, viz., into those destitute of petals (Apetalæ); those with distinct calyx and corolla, the petals being united (Monopetalæ); and those also having calyx and corolla, with all the petals free from one another (Polypetalæ). Each of these groups is subdivided into three classes, based on the relative position of stamens to ovary (in the case of the Monopetalæ of corolla to ovary). Since in the Dicotyledones with unisexual flowers it was impossible to indicate the relative position of stamens and ovaries, a special class (Dielines irregulares) was set aside for them. The institution of this last class does not mark an advance towards a natural system; whilst the limitations of the other classes in respect of the relative positions of stamens to ovary is cumbrous and unnatural, still they are less artificial than those of the Linnean Sexual System. The distinctive features of the system of de Jussieu are the broad characters upon which the families are based—the whole structure of the plant being taken into consideration—and especially the recognition of Monocotyledons and Dicotyledons as equivalent groups of Flowering

¹ A. L. DE JUSSIEU'S SYSTEM OF 1789.

		Class.
Acotyledones		I.
Monocotyledones	{ Stamina hypogyna	II.
	perigyna	III.
	epigyna	IV.
Dicotyledones	{ Stamina epigyna	V.
	perigyna	VI.
	hypogyna	VII.
	{ Corolla hypogyna	VIII.
	perigyna	IX.
	epigyna { Antheris connatis	X.
	distinctis	XI.
	{ Stamina epigyna	XII.
	hypogyna	XIII.
	perigyna	XIV.
	Dielines irregulares	XV.

Plants. A. P. De Candolle¹ (1778-1841) in his *Théorie Élémentaire de la Botanique, ou Exposition des Principes de la Classification naturelle* (published 1813), distinguished between cellular and vascular plants (Cellulares and Vasculares). The former are constructed of cells alone, whilst in the latter vessels also are met with. The cellular plants were divided into those without leaves (Cellulares aphyllæ) and those provided with leaves (Cellulares foliaceæ). The vascular plants were divided according to anatomical views current at the time into those in which the vascular bundles were scattered through the stem and were supposed to originate from within (Endogenæ), and into those in which the vascular bundles were arranged in a ring and were added to from without (Exogenæ). The group Endogenæ included the Vascular Cryptogams (Endogenæ cryptogamæ), forms destitute of flowers, and the Monocotyledons of de Jussieu (Endogenæ phanerogamæ). The Exogenæ, the equivalent of de Jussieu's Dicotyledones, were divided into those with a simple perianth (Monochlamydeæ), and those with a distinct calyx and corolla (Diplochlamydeæ). The latter are further subdivided into three groups: the Corollifloræ, in which the petals are united into a continuous corolla; the Calycifloræ, in which the petals are inserted upon the calyx; and the Thalamifloræ, in which the petals are free and inserted upon the floral receptacle. Although De Candolle based his system upon characters essentially different from those used by de Jussieu, and although in both systems there are many deviations in the limitations of the classes and families, there is on the whole an agreement in many essential particulars. Especially may we note the recognition of Monocotyledons and Dicotyledons (though under different names) as the two contrasting main divisions of Flowering Plants. And further, that the Cellular and Vascular Cryptogams are sharply distinguished from one another. The main groups, the Cellular and Vascular Cryptogams, the Monocotyledons and Dicotyledons, are met with (under various names) from this time onwards in all later schemes of classification; and, so far as we can tell, appear to constitute so many natural groups—groups, that is, of which the members are all more nearly allied by descent to one another than to the members of the other groups.

Following De Candolle many Botanists elaborated schemes of classification during the first half of the nineteenth century; these included Reichenbach, Oken, Agardh, Martius, Brongniart, Bartling, Endlicher, Lindley, and many others. To the non-botanist, recognizing the fact that there can be but one real natural system

¹ A. P. DE CANDOLLE'S SYSTEM.

I. VASCULAR OR COTYLEDONOUS PLANTS.

1. EXOGENE OR DICOTYLEDONS.

- A. Perianth double (calyx and corolla).
Thalamifloræ (petals distinct, inserted on the receptacle).
Calycifloræ (petals free and inserted on the calyx).
Corollifloræ (petals united together).
- B. Monochlamydeæ (perianth simple).

VASCULAR OR COTYLEDONOUS PLANTS

(continued).

2. ENDOGENÆ OR MONOCOTYLEDONS.

- A. Phanerogams (= true Monocotyledons).
- B. Cryptogams (= Vascular Cryptogams and Naiadaceæ).

II. CELLULAR OR ACOTYLEDONOUS PLANTS.

- A. Foliaceæ (leafy=Mosses and Liverworts).
- B. Aphyllæ (not having leaves=Thallophytes.)

of plants, this great variety of specialist opinion is somewhat surprising, and tends to shake his confidence in all botanical systems. But it must be remembered that in the development of a natural system the imagination plays a much more important part than in the elaboration of an artificial one, nor can prevailing currents of thought, or the particular habit of mind of the observer, be without their influence. Very prominently does this appear in the case of the Botanists who came under the influence of what has been termed nature-philosophy during the early portion of this century. Thus Reichenbach and Oken proposed systems which can only appear to us absurd; but it would be wearisome and useless to follow their absurdities in detail.

The system of classification proposed by Endlicher¹ (1805-1849), and published in his *Genera Plantarum secundum ordines Naturales disposita* (published 1836-1840) is based on the systems of de Jussieu and De Candolle. In it 6838 genera, arranged in 277 families or orders, are included. Here for the first time are the Coniferæ and Gnetaceæ distinguished as a special group, and designated as Gymnosperms. Here also is that group of cellular plants known as the Thallophyta carefully distinguished into three series, the Algæ, Lichens, and Fungi. But we still find these groups treated as equivalent to the Horse-tails, Ferns, Lycopods, &c.: so also with the Gymnosperms, they are not treated as a distinct subdivision, but only as a class of Dicotyledons (Acramphibrya), the other classes of which are the Apetala, Gamopetala (= Monopetalæ), and Dialypetala (= Polypetalæ).

In fairly recent times Bentham and Hooker,² in their well-known *Genera Plantarum* (published 1862-1883), follow essentially the systems of De Candolle and Endlicher. They assemble all flowering plants (100,220 species) into 8417 genera, and these under 210 families or orders. Of these orders 3 belong to the Gymnosperms, 35 to the Monocotyledons, 36 to the Monochlamydeæ, 46 to the Gamopetalæ, and 90 to the Polypetalæ.

¹ ENDLICHER'S SYSTEM.

I. THALLOPHYTA (no opposition of stem and root).

PROTOPHYTA.

Algæ.
Lichenes.

HYSTEROPHYTA.

Fungi.

II. CORMOPHYTA (opposition of stem and root).

ACROBRYA (stem growing at the point only).

Anophyta (Liverworts and Mosses).
Protophyta (Vascular Cryptogams and Cycads).

Hysterophyta (certain parasites, Balanophoreæ, Rafflesiaceæ, &c.).

II. CORMOPHYTA—Continued.

AMPHIBRYA (stem growing at the circumference).
Includes Monocotyledons.

ACRAMPHIBRYA (stem growing at both point and circumference).

Gymnosperma (ovules naked, fertilized directly from the micropyle).

Apetala (Perianth 0, rudim. or simple).

Gamopetala (Perianth double, petals united).

Dialypetala (Perianth double, petals free).

² THE MAIN DIVISIONS OF BENTHAM AND HOOKER'S SYSTEM

(FOR FLOWERING PLANTS ONLY).

DICOTYLEDONES.

Polypetalæ.
Gamopetalæ.

DICOTYLEDONES—Continued.

Monochlamydeæ.
Gymnospermæ.

MONOCOTYLEDONES.

Though the grouping of Dicotyledons (according to the characters of the perianth) into Monochlamydeæ (= Apetalæ), Gamopetalæ (= Monopetalæ), and Polypetalæ (= Dialypetalæ), is very generally recognized to be an unnatural one, it is no easy task to replace it by a better one. The families belonging to the great group Dicotyledons show the most multifarious relations to one another. An arrangement, based on the assumption that these families have been developed one from another, is not discoverable; whilst an arrangement in linear series is as unnatural as one resembling a tree with its branches. Very appropriate was Linnaeus's comparison of the limitations of these families with the dovetailing of the frontiers of countries on a map. One family stands in touch with two, another with three, others again with four or more allied families. This contact or relationship occurs on the most various sides. Some families are extremely large and comprehensive, others relatively small, and, as it were, jammed in between them: whilst others resemble scattered islands off the coast of a continent.

Well worthy of consideration is the system of Alexander Braun,¹ published in 1864 in Ascherson's *Flora der Provinz Brandenburg*. Though the division of Dicotyledons into Apetalæ, Sympetalæ, and Eleutheropetalæ suggests at first sight the classifications of de Jussieu and Endlicher, there is a difference, and an important one. A large number of the families included by the older Botanists in the Apetalæ are here placed in the Eleutheropetalæ. With the Eleutheropetalæ are ranked those plants "in which calyx and corolla are typically present, the latter consisting of separate petals". They are ranged in 24 Alliances or Cohorts—Hydropeltidinae, Polycarpiceæ, Rhœadinae, Parietales, Passiflorinae, Guttiferae, Lamprophyllæ, Hesperides, Frangulinae, Æsculinae, Terebinthinae, Gruinales, Columniferae, Urticinae, Iricocceæ, Caryophyllinae, Saxifraginae, Julifloræ, Umbellifloræ, Myrtifloræ, Thymelæinae, Santalinae, Rosifloræ, Leguminosæ. In recent times we have the systems of Eichler and Engler. They follow the lines laid down by Alexander Braun, but, carrying his method further, the group Apetalæ (or Monochlamydeæ) is entirely abolished, its members being referred in part to the Sympetalæ, and in part to the Eleutheropetalæ (= Archichlamydeæ of Engler).

During the last fifty years our knowledge of the Cryptogams constituting the group Thallophyta (founded by Endlicher, *cf.* foot-note, p. 604) has increased by leaps and bounds. Several attempts have been made to bring together the results of the various researches upon this group, and to utilize them for classificatory

¹ ALEXANDER BRAUN'S SYSTEM.

I. BRYOPHYTA.

1. Thalloidea (Algæ, Lichens, and Fungi).
2. Thallophyllodea (Characeæ, Mosses, and Liverworts).

II. CORMOPHYTA.

1. Phyllopterides (Ferns and Equisetums).
2. Maschalopterides (Lycopods).
3. Hydropterides (Rhizocarps).

III. ANTHOPHYTA (Flowering Plants).

- A. GYMNOSPERMÆ (seeds exposed).
 1. Frondosæ (Cycads).
 2. Acerosæ (Conifers).
- B. ANGIOSPERMÆ (seeds in an ovary).
 1. Monocotyledones.
 2. Dicotyledones.
 - a. Apetalæ.
 - b. Sympetalæ.
 - c. Eleutheropetalæ.

purposes. The old division into Algae, Fungi, and Lichens, based on the presence or absence of chlorophyll and on the mode of life of the forms in question, has been by many authors abandoned. Cohn in 1872 divided the Thallophytes, according to their methods of reproduction, into seven groups: Schizosporeæ, Zygosporæ, Basidiosporæ, Ascosporeæ, Tetrasporeæ, Zoosporeæ, and Oosporeæ. Sachs, in 1874, following somewhat similar lines, made four classes: Protophyta, Zygosporæ, Oosporeæ, and Carposporæ, in each of which groups both chlorophyll-containing (Algae) and colourless forms (Fungi) occur, as may be seen by a perusal of the classification quoted below.¹ Gebel (1882) returns in part to the older method and distinguishes between Algae and Fungi; but with these as groups of equal systematic importance he ranks the Myxomycetes, Diatomaceæ, and Schizophyta. The Algae he divides into Chlorophyceæ (Green Algae), Phæophyceæ (Brown Algae), and Rhodophyceæ (Red Sea-weeds); and the Fungi into Chytridiaceæ, Ustilagineæ, Phycomycetes, Ascomycetes, Æcidomycetes, Basidiomycetes. Warming (1884) returns completely to the older method, dividing the Thallophytes into Algae and Fungi, ranking the Myxomycetes with the Fungi, and the Diatoms and Schizophyceæ with the Algae. The balance of opinion at the present time, largely swayed by the views and researches of Brefeld upon the Fungi, favours a grouping of the bulk of Thallophytes into Algae and Fungi. Brefeld regards the various families of Fungi as more intimately related amongst themselves than are these families to corresponding families of Algae. That Fungi have arisen from Algae at some remote period, and have then amongst themselves undergone development along various lines, is very generally held; but the view that the different families of Fungi stand in near relationship to the several algal groups—as indicated, for instance, in the system of Sachs, (*cf.* foot-note below)—is not at present the prevalent one. And amongst the Algae, also, the attempt to classify the various forms into families according to the relative simplicity or complexity of their organs of reproduction (as Sachs suggested) no longer finds general favour. Amongst the Algae we find a number of extensive

¹SACHS'S CLASSIFICATION OF THALLOPHYTES.

I. PROTOPHYTA.	
<i>Containing Chlorophyll.</i>	<i>Not containing Chlorophyll.</i>
Cyanophyceæ.	Schizomycetes.
Palmellaceæ (in part).	Saccharomycetes.
II. ZYGOSPOREÆ.	
<i>Conjugating Cells Motile.</i>	
Pandorinææ (Hydrodictyææ).	Myxomycetes.
<i>Conjugating Cells Stationary.</i>	
Conjugatæ.	Zygomycetes.
III. OOSPOREÆ.	
Sphæroplea.	
Vaucheria (Cœloblastææ),	{ Saprolegniææ.
Volvocinææ.	{ Peronosporææ.
Edogonææ.	
Fucoideæ.	
IV. CARPOSPOREÆ.	
Coleochætææ.	Ascomycetes (including Lichens).
Floridææ.	Æcidomycetes (Uredinææ).
Characeæ.	Basidiomycetes.

groups, within the limits of each of which all stages of complexity in reproduction occur. The attempt to string together forms agreeing in reproductive methods makes it necessary to break up groups which on general grounds seem to be natural families. And as it is a natural system that we are striving after, systems like that of Sachs (which may be compared to the artificial sexual system of Linnaeus) must be abandoned. That the publication of the Sachsian system in his widely-read "Text-book" has done great service to Botany there can be no doubt; it has stimulated thought and observation, and has led more speedily than would otherwise have been the case to the establishment of broad and probably sound views as to the relations of the Thallophytes. However, the Myxomycetes, approaching as they do certain groups of the animal kingdom, are kept apart from the rest of the Thallophytes in the most recent system.

The classification of plants according to their similarity of structure—species into genera, genera into families or orders, families into alliances or cohorts, these into classes, and classes into two chief branches or phyla, the Cryptogams and Phanerogams—leads to the presumption that these two chief branches have arisen from a common stock, have diverged from a common stem. A consideration of all animal and plant forms similarly leads us to the belief that the main stems of the Animal and Vegetable Kingdoms, respectively, meet at their points of origin. By studying systems of classification drawn up on paper and restricted to two dimensions of space, we involuntarily conceive the classes and orders of the vegetable kingdom, as a tree which continually branches, finally ending in thousands of twigs which represent the various species. Such is, rightly or wrongly, the conception of all Botanists who have concerned themselves with the construction of a natural system. They only differ in so far that some regard the Thallophytes as standing at the base, and derive from these the Liverworts and Mosses, from these the Ferns, &c., and so on to the Gymnosperms and Angiosperms; whilst others make a subdivision of the main trunk at once into Cryptogams and Phanerogams, each of these continually branching according to the various classes and families. Others again, whilst conceiving the whole vegetable kingdom as having a common origin, regard this as the centre of a sphere, and that the several phyla and classes radiate out from this, producing numerous branches and twigs at the surface of the sphere. Each of these hypotheses presupposes, in the first instance, the existence (or spontaneous generation) of a few Thallophytes of extremely simple structure which have become differentiated, *i.e.* given rise to more complex offspring which form the beginnings of the branches of the tree. To this kind of development of a tree-structure, the terms Phylogenesis or Phylogeny (from *φύλη*, a tribe; and *γεννάω*, to produce) is given. Obviously, not only the original forms possess the capacity of differentiating, but their offspring also, and so on through the entire tree. But views are divided as to whether this continued differentiation follows a predetermined plan, is due to definite inherent forces, or whether it may not be restricted in this sense and due to other and external causes.

That a natural system has been evolved along lines resembling the ramifications of a tree, which commenced with simply organized structures and terminated with the most complex ones, finds a certain confirmation when the history of development of the individual (ontogeny, from *ὄν*, *ontos*, being; and *γεννάω*, to produce) is compared with its position upon the phylogenetic tree. As we know, the greatest of all flowering trees begins its existence as a single protoplasmic mass. This surrounds itself with a cell-wall and increases in size and complexity at the expense of nutriment derived from its environment. Gradually cells and tissues arise and the young organism becomes segmented into an axis and appendages. These, again, assume the most varied forms corresponding to a subdivision of labour. Ultimately the uppermost and last-produced members of the plant are transformed into flowers and fruits. It is thought that, just as a plant is gradually differentiated in this way so have all plants undergone a similar transformation, step by step. The egg-cell, the starting-point of the individual, may be compared to a Myxomycete, the cell-complex which arises from the egg-cell after fertilization to a Thallophyte, the segmented axis and appendages of the seedling to a Vascular Cryptogam, and the complete plant-body, finally, to a Flowering Plant.

This comparison, like so many others which captivated the imaginative faculties in the days of the speculations of nature-philosophy, has found many adherents; indeed, it has served as dogma and guiding light in many investigations. But it is difficult to harmonize it with other theories well-proved by experience. The main burden of this comparison (known as the "Recapitulation-theory") is that the vegetable kingdom as a whole has undergone a developmental history and transformation resembling that of a single member of the group of Flowering Plants. But first it must be asked, what is the meaning of metamorphosis in the individual, and what object has been attained by it? Though the actual processes taking place in the living protoplasm in metamorphosis are unknown, this much seems certain: That these changes occur along lines sufficiently well indicated; that the fashioning of the successive stages of any given species is accomplished according to a definite plan; that external influences, such as soil and climate, do not permanently affect this plan; and that consequently the plan of construction of these successively appearing stages is laid down in the protoplasm itself. The ultimate object of metamorphosis in plants is the production of fruit: and with the formation of an ovary the metamorphosis ends, the fertilized egg-cell beginning the metamorphosis all over again, *i.e.* it is the starting-point of a series of transformations along identical lines. And this applies equally to the Apple-tree and to the Palm, to the Pine, the Horse-tail, the Moss, the Bladder-wrack, Stonewort, to the Mould, and to the simplest of green Algae. Only in the last-named forms are the intermediate stages fewer than in the first-named. But it will hardly be suggested that the latter have not on this account attained the end in view. Simple plants whose fertilization and fruit-formation is accomplished under water, whether it be on inundated land, in the mud of a river, or at the bottom of a lake, attain this end without a complex metamorphosis of petals and stamens; whilst many

of the denizens of the ocean have no need of segmentation into stem and leaf. Indeed, such a metamorphosis for this purpose would be a disadvantage, anything but a progressive development. Similarly is it inconceivable, from all we know of the relations between external conditions and the form of an organism, that a Fern (for instance), unable to accomplish its fertilization in dew or rain-water, should in consequence depart from its usual habit and strike out a new line of metamorphosis. Thus we may conclude¹ that the development of the individual (Ontogeny) cannot be regarded as an epitome of the ancestral history or line of descent of that individual, and, further, that ontogeny gives no support to the assumption of a ramifying phylogenetic tree starting with simple forms and ending with complex much-differentiated ones.

The results of developmental investigations showing a marked similarity in the form of organs serving similar purposes in the most different groups of plants have been brought forward in support of the assumption that Flowering Plants have arisen from simple Cellular Plants by a series of progressive transformations. Though these organs are in some groups of more simple, in others of more complex structure, their similarity is unmistakable; it is upon this that the view is widely based that organisms exhibiting similar organs have been derived from one another. But this inference is inadmissible. The similarity in question finds a simpler explanation as the expression of the attainment of a common object. Thus fertilization consists in the coming together and uniting of two portions of protoplasm which have originated at a distance from one another; the similarity of ways and means in attaining this object are obvious. In one case water is employed as a means, in another the air. There is, truly, a difference in detail, but the general similarity remains. From this general similarity all we are justified in inferring is that the organisms in question all reproduce themselves by fertilization, not that they have a common origin.

This conclusion leads to the question whether, in view of the diversity of the organs of fertilization, several distinct stems of plants may not have co-existed all along. We know from observation and experiment that new forms do not as a rule arise from offshoots, but from fruits. New groups of plants might thus (so it was said) arise from existing ones solely by the sexual method. Complex Thallophytes might arise from the fruits of simpler ones, Ferns from the fruits of Mosses, and so on. Assumptions of this kind belong to a period at which the phenomena of fertilization and fruit-production, especially in the Cellular Plants, were only very imperfectly understood. No Botanist nowadays would suggest the possibility of a *Spirogyra* or a *Ulothrix*, or an *Eldogonium*, or a Stonewort, arising from the fruit of a *Vaucheria*. It might well happen that a new species could arise by the crossing of two dichogamous species of *Vaucheria*, but this new form would be essentially a *Vaucheria*, and its methods of fertilization would be essentially similar to that of its parent-forms. It is likewise as impossible for the male protoplasm of a *Vaucheria* to enter the chamber in which the conjugation of the

¹ See editorial note prefacing this volume.

sexual cells of *Spirogyra* takes place (*cf.* vol. i. Plate I. fig. 1), or for this spermatoplasm to fuse with the gametes of *Ulothrix* (*cf.* p. 49), as for the gametes of *Ulothrix* to enter and fuse with the egg-cell of a *Vaucheria*; no new group of plants could have arisen in this way. We may conclude then that plants belonging to groups with a marked diversity in their sexual characters have not arisen from one another, but belong to stems which have co-existed as distinct types from the first.

Nor must we omit to notice the observations which have been made in regard to symbiosis and the inter-relations of green and non-green plants. It has already been pointed out (vol. i. pp. 263, 264) how that the continuation of plant-life, and indeed all life, is dependent on the activity which saprophytic plants exhibit in the decomposition of dead organisms. Green plants could not exist independent of colourless saprophytes, nor these latter without green plants. This must ever have

been the case, and it must so remain.

We may then draw another conclusion, viz. that those colourless plants which by their activity bring about the decomposition of green plants cannot have arisen from green plants,

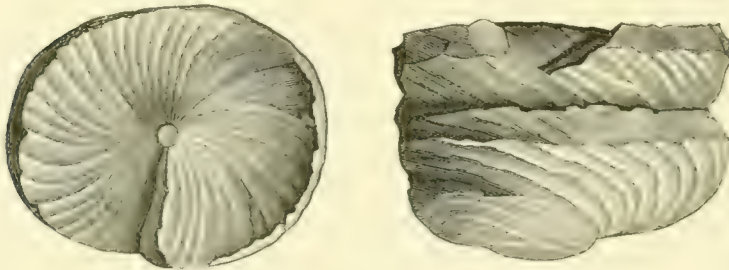


Fig. 365.—*Spirophyton* from the Upper Devonian.

but that from the beginning they have belonged to a distinct stem.

It is to Palæontology that we must look for the most trustworthy solution of the question as to whether numerous plant-stems have existed side by side from the first, or whether the groups which at present co-exist have in process of time branched forth from a single stem. Were it a fact that those forms which show a far-reaching division of labour, and a complex structure of organs, which we term "higher plants", have arisen from others of very simple mode of life and possessing a simple structure and which are known as "lower plants", then should we expect the earth to have been covered formerly by lower plants alone. And then, following this epoch, would have come a time when plants would have existed which might have served as the starting-points of the later-appearing distinct groups. We should expect to find in those strata of the earth's crust regarded by geologists as the oldest of all nothing but the remains of very simple Thallophytes, then, following these, Wracks, Red Sea-weeds, and Lichens, and after these Stoneworts (*Chara*), Mosses, or some other type of plant which, having given rise respectively to Stoneworts and Mosses, has, after this differentiation, become extinct.

From the graphite, which is looked upon as the oldest trace of vegetable life on the earth, unfortunately we obtain no conclusive evidence on this matter. From its presence on slate mountains together with crystalline limestone and pyrites

we might conclude that it originated from plants adhering to the limestone reefs formed by animals or from sea-plants which lived on the borders of these limestone cliffs. Where graphite is found in greatest quantity one is tempted to think it might have been derived from peat moors. As we have said, all these are merely suppositions, for since the carbon, lime, and silicates have become crystalline all the points for the determination of the families to which the graphite-forming plants belonged are lacking. It might be noted here, by the way, that although graphite does indeed furnish the oldest traces of plant-life on the earth this does not prove that the plants which gave rise to it were necessarily the first which



Fig. 366.—*Riella helicophylla* growing under water. Enlarged.

existed there. It is doubtful whether the rock which is associated with graphite formed the first hard crust of the earth. Much more probably this rock was composed of other broken rocks just as it has itself been again demolished, furnishing the material for new strata.

The shapes of vegetable remains from palæozoic formations are fairly easily recognizable. Those which were formerly regarded as fossil Sea-wracks have indeed been more recently interpreted as the trails of worms and medusæ, but some of them are without doubt the remains of Sea-wracks. The only other known lowly plant which at that time had an aquatic habit is the curious *Spirophyton*, the so-called Cock's-tail Alga (see accompanying fig. 365). This, though some regard it as of purely inorganic origin, may perhaps be regarded as a submerged Liverwort; at any rate it is not without resemblance to *Riella Reuteri*, which at the present time lives in the Lake of Geneva, and to the Algerian *Riella helicophylla* (see fig. 366). No trace is to be found of Thallo-

phytes which may have existed on land, but we have huge tree-like Vascular Cryptogams with trunks, fronds, and leaves which are to be placed side by side with our present-day Equisetums, Ferns, and Lycopods. Cycads and Conifers also are not absent from the Coal Measures. No Angiospermous flowering plants have hitherto been demonstrated in these strata, but it would be foolish to regard this fact as a proof that neither Thallophytes nor Angiosperms flourished at this period. That which has been preserved to us from this time certainly forms but a small fraction of the old vegetation, and is restricted apparently to the flora of peat-moors which were just as poor in species and just as monotonous as they are to-day. The plants which at the present time predominate on the moors are still the Equisetums, Ferns, Lycopods, and Conifers, and, in tropical regions, the Cycads; only a few species from each group, but standing in thousands side by side and aggregated into dense communities. Anyone who has worked out the history of these moors knows that the soil must have been prepared for these plants by other growths. *Equisetum limosum*, *Aspidium Thelypteris*, *Lycopodium inundatum*, &c., do not flourish in soil poor in humus; in order to obtain their requisite food and to develop they require soil which is saturated with the dead remains of earlier settlers. Experience tells us that the plants which appear as the first inhabitants belong to widely different groups (see vol. i. p. 268). Now if we hold to the view that the formation of peat-moors in long-past ages occurred just as in the present day, we must assume that the colonies of Equisetums, Ferns, Lycopods, and Cycads were preceded by other plants which, as the first settlers, prepared the soil. We cannot indeed determine from the surviving remains to which groups these first settlers belonged: but, looking back on the history of our present peat-moors, it seems not improbable that among them were both Thallophytes and Angiospermous flowering plants.

The fact that the fossil remains of Equisetums, Lycopods, and Cycads, which spread so widely over the peat-moors of palæozoic times, have reached us in such good condition is explained by the presence of humus-acids, which are formed universally in the peat (see vol. i. p. 263). There are four conditions which render it possible for a plant to be preserved as a fossil: humus-acids form the first; the second is the resin which exudes from the pine-wood and forms amber; the third is mud and sand brought by floods; and the fourth the silicification and calcification of the cell-wall or the formation of a lime incrustation which is precipitated from calcareous water on to the various parts of the plant. It is certain that these four conditions have always been effective, but it is doubtful whether all the fossils formed in the fourth manner at all periods have remained. For many older strata have long been destroyed and used in the building up of younger layers, and many risings and sinkings of these strata have taken place. It would indeed be difficult to find a single place on the earth's surface which has not been repeatedly above and under the sea. Much that might lead us to definite conclusions at present lies inaccessible to us, covered with immense masses of water at the bottom of the sea, and the view has actually been suggested from studies made on the few accessible

and closely investigated spots on the earth's surface that the fossil remains found there are not more than a minute fragment of the vegetation of periods long elapsed.

With these remarks we might mention that it is not beyond the range of possibility that, in addition to the Vascular Cryptogams, Cycads, and Conifers growing on peat-moors, plants of other habitats, especially those of fresh and salt water, or perhaps of sand-dunes and river-banks, might be found in the strata of palæozoic times. But no one would doubt that among these would be Angiospermous Phanerogams, and this throws some light on plant remains which have come to us from the mesozoic period. For example, in the upper layers of the chalk we find, in addition to the plants of peat-moors, the inhabitants of a luxuriant forest-flora of Angiospermous flowering plants. There are Planes, Birches, Beeches, Oaks, Poplars, Willows, Fig and Laurel trees, Maples, Ivy and other Araliaceæ, Bread-fruit trees, Tulip-trees and Magnolias, Cherry-trees, and Leguminosæ of the division Cæsalpinieæ, Palms, Rushes, and Grasses. If we do not believe in the theory that these Angiosperms were first created in the mesozoic period, and still less in the greater marvel that they have sprung from the Vascular Cryptogams, Cycads, and Conifers, we are forced to the conclusion that they too must have existed as far back as the palæozoic time. It is to be specially noted that not the slightest trace of intermediate or transitional forms which might connect the aforesaid Angiospermic Phanerogams with the Gymnosperms or with the Vascular Cryptogams has been found. One leaf is immediately recognized as belonging to a Tulip-tree, a second to Maple, a third to a Fig-tree, a fourth to a Palm, &c., but no plant has been discovered anywhere which would perhaps form a connecting link between the Palms or Figs and the Conifers or Vascular Cryptogams.

Even a cursory glance at the plant-forms named shows that they were members of mixed forests. It may be assumed, however, that other plant communities peopled the earth at the same time as these forests. The rocky terraces and boulders, as well as the flat dry land, were certainly not destitute of vegetation. Nor is it surprising that no fossil remains of the inhabitants of these places have remained. The under-shrubs and herbs of a dry soil decompose immediately after their death, and leave behind only formless humus, which mixes with the soil. Just as little fossil remains will reach posterity of the Lichens and Mosses, Pinks and Composites, Saxifrages and succulent plants which inhabit the rocks on the dry mountain-slopes at the present day, as of the Tulips and Irises, Umbelliferae and Saltworts of the steppe-flora: and a great mistake would be made if, millions of years afterwards, it were reasoned from the lack of fossil remains of these plants that they could not have existed in our time. It would be just as wrong for us to argue from the absence of such plants in the strata of earlier periods that they had never existed in those times. The same thing applies to most fresh-water and marine Alge, and to the numberless saprophytes which effect the destruction of dead animal and vegetable bodies above and under water, and thus maintain the eternal cycle of life as a whole. Of the first-mentioned the only fossil remains which can be recognized

are those of Diatoms, whose cell-wall is transformed into an imperishable siliceous frustule, together with those Florideæ which provide themselves like corals with a calcareous skeleton, and some tough Sea-wracks. It is, however, a very significant fact that the innumerable fossil Diatoms which come to us in so-called tripoli-powder and Diatom-earth, and the many calcareous Florideæ which come down to us as Nullipore banks are deceptively like those living at the present day, that these groups have remained unaltered for eons, and that no form has been discovered in any of the older strata which could be regarded as a link with another group. No fossil remains are known beyond doubt to exist of the numerous aquatic plants with delicate cell-walls which perish as rapidly as they develop, of the *Sphærella* species which give a red colour to rain-water and to the snow-field, of the microscopic Desmids, of the green filaments of *Spirogyra*, of the remarkable green tubes of *Vaucheria* pictured in plate I., &c. Some woody *Polyporus* species of Fungi have reached us, but in forms which look very like those at present growing on old tree-trunks. Some species of Moulds have been preserved in amber. I have before me a piece of amber in which insects are imbedded; from one of them spreads a web of mycelial threads which doubtless belonged to some mould-like Fungus such as to-day attacks various insects. The mycelium of various Fungi, also, are found penetrating the tissues of many of the fossil cryptogamic stems of the Coal Measures. This fact is very instructive, since it shows that in the tertiary period, and in much earlier periods also, the relation of saprophytic plants to the dead bodies of animals and plants were the same as they are to-day. All these results taken together prove that delicate Thallophytes whose cells do not become siliceous or calcareous, or which are not inclosed in resin, cannot be preserved in a fossil condition. But no one would conclude from this that the groups to which such delicate growths belong were not represented in earlier periods.

On comparing the past and present of the Vegetable Kingdom from these points of view, more especially with regard to the question whether existing groups stood side by side in earlier periods also, or whether, in the course of time, they have sprung from a single individual or from a few spontaneously-generated individuals, we are obliged to decide in favour of the former. The so-called "higher" plants are not derived from the so-called "lower"; the groups of higher and lower plants co-existed from the beginning side by side. But variations within the limits of each group have always taken place. New species, *i.e.* new groups of species, arose in consequence of the crossing of the species already in existence. Of these the species which were best suited to the climatic conditions of the time being survived. But the variation in the formation of new species never went so far as to do away with the characteristics of the group. We immediately recognize in the fossil Laurel-trees, Magnolias, Oaks, Palms, Grasses, Pines, Equisetums, Ferns, Lycopods, Florideæ, Diatoms, and Moulds the ancestors of the now existing species. This would be impossible if the group-characteristics had disappeared in the modifications which the species have undergone.

When I now attempt the task of stating in detail what has been furnished by

theoretical considerations, and of bringing forward the various groups which have from the beginning existed side by side, distinguishing them by the enumeration of their peculiar characteristics, I am not blind to the enormous difficulties of the undertaking. Although Palæontology, Morphology, and Physiology afford valuable results, they are not enough, and neither of the three sciences gives sufficient data for the complete solution of the problem. One of the greatest obstacles is the afore-said incompleteness of the geological record. From the existing remains we may indeed conclude on the whole that numerous groups stood side by side in the mesozoic and palæozoic periods, but the evidence of many groups which exist at the present day without transitional forms is wanting, and when we assume their existence we make use indeed of a justifiable hypothesis, but have no proof whatever. The danger, on the other hand, of establishing homologies from the similarity of an organ which is observed in groups of species now living has already been mentioned (see p. 609). Up to a certain point all organs which have similar work to perform agree with one another. This agreement is the more pronounced the greater the similarity of the conditions under which the organs have to do the work. Species of very different groups which live under water exhibit many characteristics in common: plants whose pollen-grains are transported by the wind show a great agreement in the structure and position of the parts of the flower. In the same way the form of flower-visiting insects necessitates a number of similar characteristics in the flowers visited. For example, we might instance the sweeping hairs on the style of the Proteaceæ and of the Composites, as well as certain developments which are met with in the flowers of Aroids, which are visited by small flies, and also in the Aristolochiaceæ. In spite of this consideration, however, the similarity in the structure and form of organs, both of those serving for propagation and for nourishment and growth, must obviously be kept to the forefront; similarity must always be an important factor in the limitation of groups.

As we have in the preceding chapter established the fact that each species is built up by protoplasm with a specific constitution, the question might be propounded whether each plant-group has not something in common in this respect. Many observations argue differently for this view. It has been repeatedly stated that the Moulds, Oscillatoricæ, Sea-wracks, Stoneworts, &c. give off a scent which, although it differs according to the species, is yet very similar upon the whole, and that one is justified in assuming a specific constitution of the protoplasm in each of these groups on this account. Moreover, the scent which the Mosses exhale is found in no other group of plants. The same is true of Ferns. The delicate fronds of the tropical Filmy Ferns exhale the same peculiar scent as the larger Ferns of our forests. The Coniferæ, Umbelliferæ, Labiateæ, Leguminosæ, and Cruciferæ exhibit similar conditions. Is it not also a striking phenomenon that the parasitic Fungus *Cronartium asclepiadeum* should settle on *Cynanchum Vincetoxicum*, as well as on *Gentiana asclepiadea*, i.e. upon two plants which the Botanist certainly places in different families, but which he regards as belonging to the same alliance? To these facts many others might be added, especially with regard to the choice of

vegetable food by animals. But our knowledge in this respect is so fragmentary and uncertain that for the present we cannot make use of these conditions in the limitations of the groups.

The capacity for sexual union is of the utmost importance in defining plant groups. Species which can unite sexually belong undoubtedly to the same group. Nothing can be urged against this principle, and if it could be universally applied, the division of the groups would be settled. But in this matter there are very many pros and cons. The converse of the proposition requires consideration. It will not do to say that all plants which cannot unite sexually belong to different groups. It has been shown that crossings can be successfully effected in Orchids which all Botanists regard as members of different genera, but, on the other hand, it is demonstrated that crossings between very similar species of the Umbellifer family lead to no fruit formation. No one, however, would conclude from this that these Umbellifers belonged to different groups. On reflecting in what a small number of flowering plants the fertilizing process has hitherto been observed, and remembering that the fertilization of many Thallophytes is still totally unknown, the hope of being able to utilize these conditions in limiting the groups becomes very much lessened.

In the review of the various groups of the vegetable kingdom which follows¹ no attempt is made to present the groups in the form of an ideal natural system. So far as the Thallophytes, Bryophytes, Pteridophytes, and Gymnosperms are concerned, there is a very general consensus of opinion amongst Botanists, and the serial arrangement here followed is in harmony with it. But as regards the Angiospermous flowering plants, and in particular the Dicotyledons, it is as yet too early in a book of this nature to embody all the most recent suggestions as to the affinities of the various families. Attention was drawn on p. 605 to the system of Alexander Braun, and it was pointed out that he was the first to try and break up the large and unsatisfactory class Monochlamydeæ or Apetalæ, and to relegate its families in part to their true position. This attempt has been very fully carried out by Eichler (1883), and by Engler (1892): these two Botanists admitting only two classes of Dicotyledons (Choripetalæ or Archichlamydeæ and Sympetalæ). But as yet many of their placings of individual families are but tentative, and we may well wait a few years for a system on these lines to settle down into more or less permanent form. An instance of too hasty rearrangement of a natural system to meet recently discovered facts may be quoted here. In 1891 Treub discovered that *Casuarina* possessed chalazogamic fertilization, and in 1892 Engler (following Treub) separated *Casuarina* from all other Angiosperms as the sole genus in a new class Chalazogamæ. Since then it has been found (see p. 413) that chalazogamic fertilization is much more general than was at first supposed, and that in the group Amentaceæ it is widely spread, though by no means of universal occurrence. To break up the Amentaceæ in the drastic manner involved, if the class Chalazogamæ be maintained, seems a most

¹ Cf. editorial note at commencement of this volume.

undesirable and unnatural thing to do: it will on the whole be best to abolish a special class of Chalazogams, and, if thought necessary, to rearrange the families which constitute the Amentaceæ, but not to sever them from one another. For the Angiosperms we shall in the main follow the arrangement of the well-known *Genera Plantarum* of Bentham and Hooker, though we reserve our freedom to deal with certain families as seems well to us.

The vegetable kingdom we divide first into four main divisions or *phyla*: (1) The Myxothallophyta, including the Myxomycetes only, a group standing apart from (2) the Thallophyta, which include the various classes of Algae and Fungi. Then follows (3) the Archegoniata, forms possessing archegonia and fertilized by motile spermatozooids, and including the Liverworts and Mosses, and the series of the Ferns (Phyla (1) (2) and (3) constitute what are usually referred to as "Cryptogams"), and (4) the Phanerogamia or flowering plants, fertilized by means of pollen-tubes. They fall into two sub-phyla, Gymnosperms and Angiosperms, and the latter into two classes, Monocotyledons and Dicotyledons. Finally we have the 3 sub-classes of Dicotyledons—Monochlamydeæ, Monopetalæ, and Polypetalæ. Here, in outline, is the system:—

(1) MYXOTHALLOPHYTA, containing 1 class only.

(2) THALLOPHYTA, containing 5 classes.

- I. *Schizophyta*.
- II. *Dinoflagellata*.
- III. *Bacillariales*.
- IV. *Gamophyceæ*.
- V. *Fungi*.

(3) ARCHIGONIATÆ, containing 2 classes.

- I. *Bryophyta*.
- II. *Pteridophyta*.

(4) PHANEROGAMÆ, containing 2 sub-phyla.

A. GYMnosPERMÆ.

B. ANGiosPERMÆ, containing 2 classes.

I. *Monocotyledones*.

II. *Dicotyledones*, containing 3 sub-classes.

- a. *Monochlamydeæ*.
- b. *Monopetalæ*.
- c. *Polypetalæ*.

Each class (or sub-class) is further divided into a number of cohorts or *alliances*, and each of these alliances into orders or *families*. The alliances will be taken one by one in the following pages, their main characters generally indicated, and the families which they comprise enumerated. It will not be possible within the limits of this book to deal with the several families in at all a comprehensive manner, though the endeavour will be made to point out structural and other characters of interest, and where certain genera or groups of genera have a special interest these will be alluded to. No attempt is made to observe any due sense of proportion in treating of the different alliances. Thus a small alliance containing but few members of especial interest will receive more detailed consideration than one vastly

larger, the numerous representatives of which are unrelieved in their monotony. This method, truly, is an unconventional one, but in view of the restrictions of space, perhaps better suited to our purpose than any other.

PHYLUM 1.—MYXOTHALLOPHYTA.

Organisms destitute of chlorophyll, whose vegetative state consists of a mass of naked protoplasm (plasmodium). Reproduction by spores, from which arise swarm-spores or myxamœbæ, which unite again into plasmodia.

Alliance I.—Myxomycetes, Slime-Fungi.

For the most part saprophytic upon dead organic and especially vegetable substances; they occur chiefly on accumulations of the dead parts of plants—leaves,

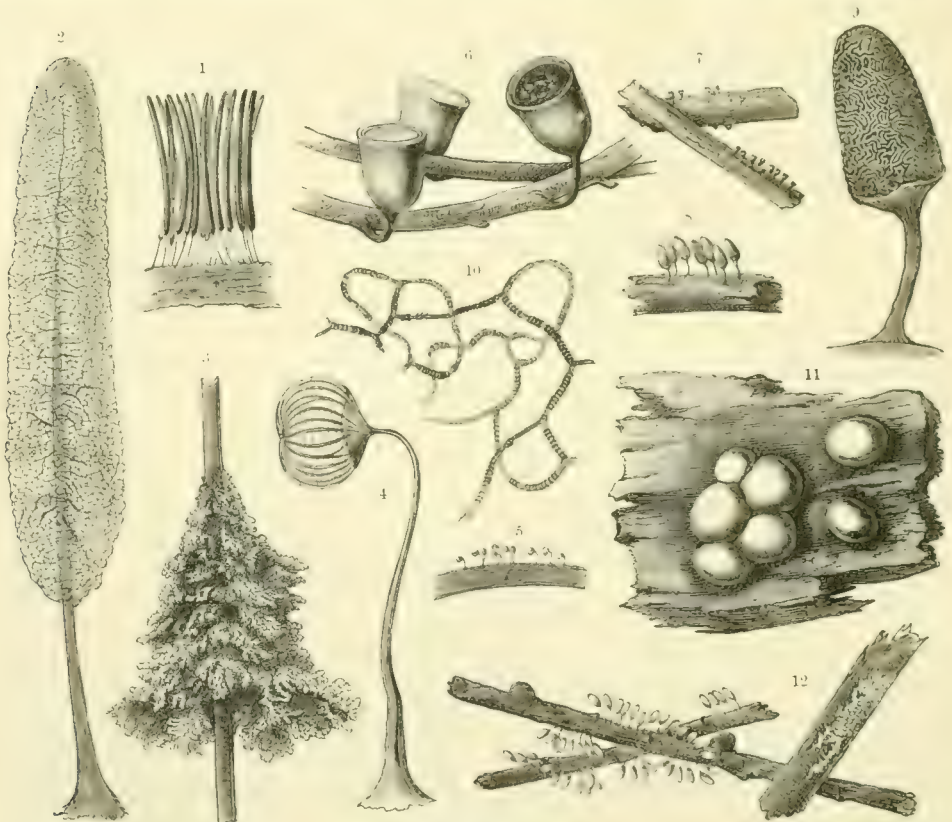


Fig. 367.—Myxomycetes.

¹ A group of sporangia of *Stemonitis fusca*. ² A single sporangium; $\times 6$. ³ Dendritic mass of sporangia of *Spumaria alba* on a Grass leaf. ⁴ Sporangium of *Dictydium cernuum*; $\times 25$. ⁵ A group of sporangia of the same. ⁶ and ⁷ Sporangia of *Craterium minutum*; $\times 25$. ⁸ Sporangia of *Arcyria punicea*. ⁹ A single sporangium; $\times 10$. ¹⁰ Part of the net-like capillitium of the same; $\times 160$. ¹¹ Fructification of *Lycogala epidendrum* on a piece of wood. ¹² *Leocarpus fragilis*; a plasmodium on the right; several sporangia on the left.

tan, rotting wood, and the like; they are rarely parasitic. Their life-history is as follows:—On the germination of the spores the membrane bursts, and a slimy, nucleated mass of protoplasm escapes, which either swims in water by means of a

single flagellum, or creeps about on a damp substratum; these motile bodies are the *myxamœbæ*. These amœbæ increase at the expense of absorbed nutriment, and undergo repeated division. Ultimately they fuse together into masses of naked protoplasm—the *plasmodium-stage*—which creep about until spore-formation sets in. The plasmodium is transformed into the reproductive stage, numerous sporangia arising all over its surface. This stage in different cases shows the most varied structure, as may be seen by reference to fig. 367. Either the whole plasmodium is transformed into a single sporangium, as in *Lycogala epidendrum* (fig. 367¹¹), or a number of sporangia arise. A portion of the protoplasm becomes hardened to form the wall of the sporangium, whilst the contents is resolved into a mass of dust-like spores. In addition there arises in the majority of forms a sort of internal skeleton, the *capillitium*, which may consist either of a number of elongated tubes with characteristic thickenings on their walls, or these tubes may be united together into a continuous network (fig. 367²). On the bursting of the sporangium the spores are scattered and carried away by currents of air. They germinate when they reach a moist substratum, and the life-cycle is passed through anew. Under unfavourable conditions a plasmodium may become encysted, forming a transitory resting-stage. If placed in water, the plasmodium escapes from the cyst, and continues its life-history even after a lapse of several months. The substance of the membrane, whether of the sporangial wall, spores, or capillitium, does not seem to consist of cellulose, but rather of a congealed protoplasm. We see, then, that the life-history of a Myxomycete is divided into a nutritive stage consisting of naked, membraneless, protoplasmic masses, and a sporangial, spore-producing stage. In respect of their nutritive stage the Myxomycetes very nearly resemble certain groups of the Protozoa, and on the strength of this resemblance they are regarded by many Botanists and Zoologists as belonging rather to the animal than to the vegetable kingdom. In their manner of reproduction they certainly show analogies to many of the Fungi however.

Plasmodiophora Brassicæ is a parasitic Myxomycete which attacks the roots of the Cabbage, causing the disease known as "Fingers and toes" (*cf.* p. 522).

Fossil Myxomycetes are not known. About 450 species have been distinguished.

PHYLUM 2.—THALLOPHYTA.

A large and very heterogeneous collection of plant-forms is included under this term. The word (Greek *θαλλός*, and *φύλλον*) literally means plants with undifferentiated shoots, and includes practically all plants standing below the Mosses and Liverworts in complexity of organization. It is impossible to characterize positively a group, or rather a collection of groups, which shows so wide a range of organization as we find among the Thallophytes. They are often characterized negatively as plants whose bodies show no distinction between axis and appendages (stem and leaves). To such a plant-body the name *thallus* is given. But though this definition holds good for the great majority of the Thallophytes, yet there are forms (*e.g.* *Bryopsis*,

the verticillate Siphonææ, *Draparnaldia*, many of the Brown Sea-weeds) which do show a distinction between axis and appendages, though the distinction is not usually so marked as that between the stem and leaves of a higher plant. Similarly, though for the most part possessing a relatively low organization, some Thallophytes (especially the higher Fungi and certain of the Brown Sea-weeds) show considerable differentiation of structure. The *Thallophyta* consist of many divergent and more or less sharply characterized groups. These include the Green Algæ (*Chlorophyceæ*, which includes the alliances Protococcoideæ, Siphonææ, Conferoideæ, Conjugatæ, and Charales), the Brown Sea-weeds (*Phaeophyceæ*), the Red Sea-weeds (*Rhodophyceæ* or *Florideæ*), the Blue-green Algæ (*Cyanophyceæ* or *Schizophyceæ*), the Bacteria (*Schizomycetes*, here included with the last-named group in one class, the *Schizophyta*), the Diatoms (*Bacillariales*), and the Fungi. Some Botanists consider that the Myxomycetes (or *Mycetozoa*), and the Dinoflagellata (*Peridineæ*) are also plants. These last groups are almost certainly branches of the Protozoa: and though possessing certain plant-like characters (as indicated above), they show no near affinity with other plant groups. Whether they should be considered as plants or animals must therefore remain a matter of opinion.

The same may be said of certain other organisms regarded by zoologists as Flagellate Protozoa, but showing undoubted affinities with the lower forms of Green Algæ. There exists, in fact, an unbroken series of forms, connecting undoubted Protozoa, having mouths by which they eat solid food, with undoubted green plants depending entirely on soluble inorganic food. The dividing line between animals and plants is here obviously an artificial one, and is naturally drawn by different authorities at different points in the series.

The name Thallophyta, then, is given to all plant-forms below a certain grade of organization, and includes many separate and widely divergent lines of descent. The Thallophytes may be pictured as the shrubby growth around the base of the phylogenetic tree representing the plant kingdom. The lower part of the main trunk of the tree, that is to say, the line of descent by which the higher plants have originated, is probably represented by certain of the Green Algæ.

Class I.—SCHIZOPHYTA.

For the most part exceedingly small organisms, which propagate entirely by asexual methods. They consist of isolated cells, cell-filaments, surfaces, or masses. Though till recently regarded as without nuclei, these bodies have been found in a number of forms, and this view is being abandoned. They include both coloured and colourless forms: but the coloured forms never exhibit pure chlorophyll.

Alliance II.—Cyanophyceæ, the Blue-green Algæ.

Families: *Chroococcaceæ*, *Nostocaceæ*.

Includes pigmented forms in which in addition to chlorophyll *phycocyanin* is present, giving the cells a bluish, violet, or reddish tint. They occur in water or in moist places, and their cells may be united together into aggregates of various kinds. The cell-walls are usually mucilaginous, so that the cells or filaments cling together in colonies, or they are inclosed in special sheaths. The simpler forms included under the *Chroococcaceæ* are unicellular; the products of their division may either remain united into colonies or become quite free from one another. The rest are filamentous, and are included under the *Nostocaceæ*, whose filaments can become segmented into small portions which move away by a peculiar motion not yet fully understood (*cf.* vol. i. p. 40). At times also certain cells become resting-spores and can endure climatic vicissitudes. They are widely dispersed over the globe, and are met with in cold glacier-streams and have been found living in hot springs at a temperature of even 85° C. Some 800 living species are distinguished.

Chroococcaceæ.—Includes the unicellular forms. *Glæocapsa* (vol. i., Plate I. *n, o*) forms little mucilaginous colonies, often found on the moist window-panes of hot-houses. *Merismopedia* forms films on stagnant water, and *Clathrocystis* like certain of the *Nostocaceæ* (alluded to below) arises in quantity in water. A form probably referable to this group (*Dermoglæa Lini*) developed in 1874 in such quantities off the Adriatic coasts as to seriously interfere with the fishing industry. A commission was appointed to investigate the matter, but in six weeks the *Dermoglæa* vanished as suddenly as it had appeared.

Nostocaceæ are, for the most part, filamentous, though in some forms the cells may become isolated. *Nostoc* itself is common, and takes the form of irregular gelatinous colonies, which contain numerous interwoven necklace-like filaments. In some districts, owing to its sudden appearance after rain, it has received the name of "Falling Stars". This explains the allusion in the following lines from Dryden's *Ædipus*:—

"The tapers of the gods,
The sun and moon, run down like waxen globes;
The shooting stars end all in *purple jellies*,
And chaos is at hand".

A species common in China, *N. edule*, is used as a thickening for soup, and an allied form, *Hormosiphon arcticus*, abounds in the Arctic regions upon floating ice. *Anabaena Flos-aquæ*, *Aphanizomenon Flos-aquæ*, &c., appear in fresh and brackish water—sometimes in enormous quantities, and to considerable depths. The *Trichodesmium Erythræum*—another of these "flowers of the sea"—referred to at vol. i. p. 389, belongs also to this group. Very little is really known about the life-histories of these interesting plants, which so frequently appear in great quantities at or near the surface of the water and then as mysteriously disappear. But now

that systematic observations are being made of the organisms which occur at the surface (*e.g.* at the Biological station on the Plöner See, Schleswig-Holstein) we may hope that these lacunæ in our knowledge may be filled up. Recent investigations (by Klebahn) upon several of these "flowers of the sea" (*Gloietrichia echinulata*, *Anabæna Flos-aquæ*, *Aphanizomenon Flos-aquæ*, *Trichodesmium*, &c.) seem to indicate that they possess special organs of flotation designated "gas-vacuoles". It would appear that these natant forms have in consequence a smaller specific gravity than the surrounding water, and if the surface be quite unruffled tend to float, whilst any disturbance, such as waves, &c., is sufficient to cause their distribution through the upper layers of the water. Whether these "flowers" pass another stage deep down in the water is not fully ascertained. Their spores, so far as they have been observed, do not seem to possess "gas-vacuoles", and sink to the bottom. The phenomenon here indicated is not unlike that occurring in the Protozoon *Areella*, the protoplasm of which is able by secreting a bubble of gas to rise to the surface, and, by absorbing it, to cause the organism to sink. The *Oscillarias* consist of filaments of disc-like cells; they exhibit curious gliding movements, which have been already alluded to (*cf.* vol. i. p. 40). *Rivularia* is distinguished by the fact that its filaments are whip-like, ending in a fine point, whilst in *Scytonema* this distinction of base and apex is not found. They generally occur in more or less mucilaginous masses.

A number of the Schizophyceæ are associated with certain Fungi to form Lichens (*cf.* later, and vol. i. p. 244); and certain of them occur embedded in the tissues of other plants. Thus species of *Nostoc* are met with in certain Liverworts (*Anthoceros*) and in the roots of *Cycas*; and *Anabæna* in special cavities in the leaves of the Rhizocarp *Azolla*. It is not known what may be the exact physiological relations between these Blue-green Algæ and the plants they inhabit—whether they are parasitic or symbiotic.

Alliance III.—Schizomycetes, the Bacteria.

On the whole, in the matter of their structure and aggregation, present many characters in common with the Blue-green Algæ. They are, however, destitute of the characteristic pigment of that group, and pass their lives as parasites and saprophytes, obtaining their food from ready-formed organic matter. Nuclei have been distinguished in some few forms, and the cells are inclosed in a membrane which, though often mucilaginous, does not consist of cellulose. In size the cells reach very small dimensions, and may be regarded as the smallest of all plant-forms. A number of different forms are distinguished; the Cocci, consisting of minute round cells; short rod-like forms, the Bacteria; longer rod-like forms, the Bacilli; various spiral forms known as Spirillum, Vibrio, and Spirochæte; filamentous forms, Leptothrix and Crenothrix. A very common mode of occurrence of the various forms is in gelatinous masses, to which the name Zoogloea has been applied (*cf.* fig. 368²). Propagation takes place vegetatively by cell-division so long as the

conditions remain favourable for further growth. When the substratum is exhausted, &c., spores are formed which can remain for long periods—until, indeed, circumstances are again favourable for renewed development. These spores may arise either inside the bacterial cells (=endospores), the protoplasm contracting somewhat and forming a new wall around itself, or the cells may become transformed entirely into spores (=arthospores), the wall becoming specially thickened. In no case is there any sexual process. Whilst many Bacteria are only known under certain forms and are regarded as species of the genera *Micrococcus*, *Bacterium*, *Bacillus*, *Spirillum*, &c., others are known which, in the course of their development, pass through several such forms, and are termed pleomorphic. That all Bacteria are thus pleomorphic seems improbable, though the discovery that pleomorphism existed at one time led to the wildest generalizations. Large numbers of Bacteria display an active movement which, though formerly attributed to various contractions of their bodies, are now known to be due to cilia. These cilia may be borne in tufts of 5 or 6 at the two ends of the organism, as in *Spirillum Undula*, or they may be solitary at one extremity, as in the Cholera Bacterium (*Spirochate cholera asiaticæ*), or they may be scattered over the surface of the organism, as in the Hay-bacillus, *Bacillus subtilis*. It is due to the extreme fineness of these cilia that they were not recognized long ago.

Though the forms under which Bacteria occur are relatively few, their mode of life and special activity is exceedingly varied. The interest attaching to Bacteria rests largely on their effects on the substratum from which they draw their food. Taking, first, the saprophytes. These split up their substratum into simple substances. In some cases there is a complete oxidation, with production of carbon dioxide and water; in others this is only partial, as in some of the cases of fermentation, *e.g.* when alcohol is oxidized into acetic acid by the activity of the vinegar organisms *Bacillus* and *Micrococcus aceti* (*cf.* figs. 368³ and 368⁴). Or there may be a decomposition unaccompanied by simple oxidation, as in many cases of fermentation, *e.g.* as when sugar is split into alcohol and carbon dioxide. Often these operations are accompanied by the development of a foul-smelling gas, when we speak of putrefaction. The number of saprophytic Bacteria which excite characteristic splittings in their substrata is considerable. In addition to those already quoted, we may mention *Bacillus Amylobacter*, the organism of butyric acid fermentation; *Bacillus lacticus*, which causes milk to become sour; *Leuconostoc mesenteroides*, which has the power of converting large quantities of sugar into a gelatinous mass in a very short space of time. Again, in a number of forms the production of a special colouring matter is associated with the activity of the organisms, as is the case with *Micrococcus prodigiosus* (*cf.* fig. 368¹), the “blood-portent” which makes its appearance on various starchy food-stuffs, and *Beggiatoa roseo-persicina*, found on decaying vegetable matter in water, and known as “peach-mud”. Many Bacteria are parasitic in the bodies of animals, and some among them are harmless. This is the case with *Sarcina ventriculi* (fig. 368¹⁰), known only in the human alimentary canal in the form of packets of cells. Harm-

less also are a number of Bacteria found on the mucous membrane of the mouth. On the other hand, many are associated with definite diseases. *Spirochæte Obermeieri* (fig. 368⁹) is found in the blood in great quantities during relapsing fever; *Bacillus anthracis* (figs. 368⁷ and 368⁸) causes anthrax in cattle, &c.; and a great many other diseases—diphtheria, cholera (figs. 368⁵ and 368⁶), tuberculosis, leprosy, &c.—are associated with the activity of specific bacterial organisms. Nor must we omit to mention the numerous forms which occur in the soil, some of which are concerned in the process of nitrification, *i.e.* which oxidize ammonia into nitric acid, thus rendering this source of nitrogen available to higher plants, whilst others

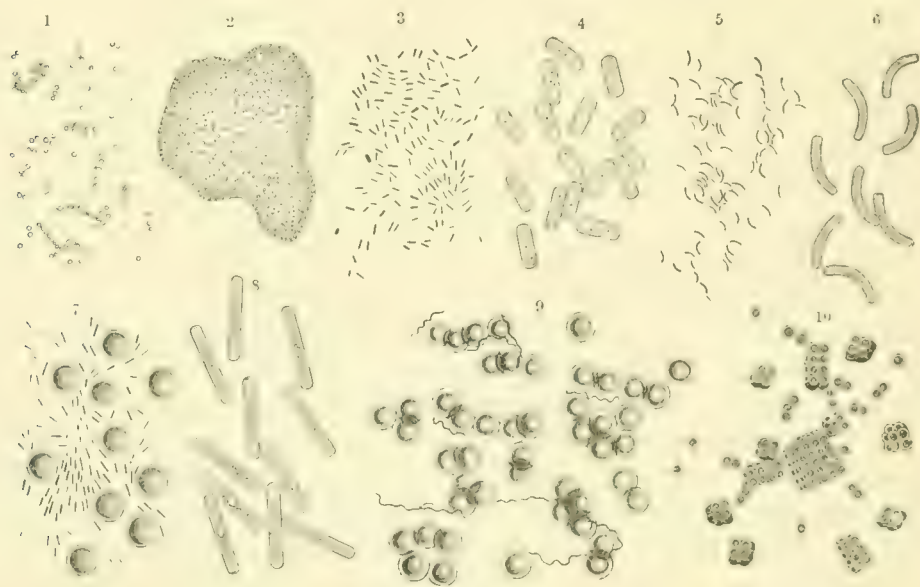


Fig. 368.—Bacteria.

¹ The "blood-portent," *Micrococcus prodigiosus*. ² Zoogloea-form of same. ³ *Bacterium aceti*. ⁴ The same more highly magnified. ⁵ *Spirochæte cholerae asiaticæ*. ⁶ The same more highly magnified. ⁷ *Bacillus anthracis* and red blood-corpuscles. ⁸ The same more highly magnified. ⁹ *Spirochæte Obermeieri* and red blood-corpuscles. ¹⁰ *Sarcina ventriculi*.
1, 2, 5, 6, 7, 9 $\times 300$; 10 $\times 800$; 4, 6, 8 $\times 2000$.

actually fix free nitrogen, as is the case with the organism occurring in the root-tubercles of many leguminous plants (*cf.* p. 521). There is no doubt this organism (*Rhizobium*, as it has been called) can store up free nitrogen, and that leguminous plants, when associated with it, obtain nitrogen not to be accounted for as combined nitrogen obtained from the soil. Curious also is the activity of the sulphur and iron Bacteria. The former (*e.g.* *Beggiatoa alba*) have the power of reducing the sulphates contained in the waters which they inhabit and of storing up sulphur-grains in their protoplasm; whilst the latter (*e.g.* *Crenothrix Kühniana*), not uncommon in water-pipes, where they often develop in enormous quantities, store up iron in the gelatinous sheaths of their filaments.

That Bacteria existed in former times, and were then, as now, the agents of decomposition, seems probable in view of the condition revealed by residues of dead

plants in the coal measures. It is thought that *Bacillus Amylobacter* has been identified in a silicified state.

Of living Bacteria a very large number have been distinguished.

Class II.—DINOFLAGELLATA, Peridinæ.

Alliance IV.

This compact group of unicellular organisms is, as has been said above, a branch of the Flagellate Protozoa. They have therefore no very near affinities with other plant groups, though the nutrition of many is thoroughly plant-like. They would come nearest to the motile (Flagellate) forms of *Protocecoideæ* (see p. 628).

The great characteristic of the group is the possession of two flagella, one directed longitudinally and attached to the anterior end of the body, the other transversely directed and often situated in a circular transverse groove. There is sometimes also a longitudinal furrow. It is this transverse flagellum which is specially concerned in movement.

There is often a cell membrane of cellulose, and the cell possesses green or brownish chromatophores containing chlorophyll and a single large nucleus.

Reproduction is effected by binary fission, usually during a resting stage of the cell.

Most of the forms are marine, and some are the cause of sea-phosphorescence.

The group is divided into two sections—the *Adinida* without, and the *Dinifera* with a transverse furrow.

Ceratium and *Peridinium* are two well-known genera.

Class III.—BACILLARIALES.

Alliance V.

Family: *Diatomaceæ*, Diatoms.

These are a large group of unicellular plants which grow both in fresh and salt water and upon moist soil. As a rule they occur together in large numbers. The protoplasm is coloured brown by a brown pigment, *diatomin*, which masks the chlorophyll which is also present. The colouring matter is restricted to special chromatophores, which may be few or numerous. The cell-wall is incrustated with silica, and is a very characteristic feature of the Diatom. The wall consists of two halves or valves (*frustules*) which fit into one another like the lid on to a pill-box. These valves are smooth or variously sculptured, dotted, ribbed, &c., and enjoy a wide popularity as microscopic objects on account of the beauty and delicacy of their tracery. Some idea of the variety and form of Diatom-cells may be obtained from the accompanying figure 369. In the colonial forms the cells are attached to the substratum directly (fig. 369¹) or by means of branching filaments (fig. 369¹¹). Others are attached to one another in zigzag chains or continuous ribbons (figs. 369¹⁵ and 369¹⁶). Others, again, are embedded in mucilage. Many of the forms

exhibit a curious creeping movement, which is explained as being due to an external sheath or to filaments of protoplasm; the median line (or "raphe") shown by certain forms (e.g. *Navicula*, fig. 369⁴) is interpreted as a narrow slit at which this external protoplasm is extruded. Diatoms propagate by continuous longitudinal division; the valves are slightly separated, and division takes place parallel to the faces of the valves. Each daughter-cell thus possesses one of the valves of the mother-cell, and they complete their integument by secreting another on the side away from it. The new valve is always slightly smaller than the other one and

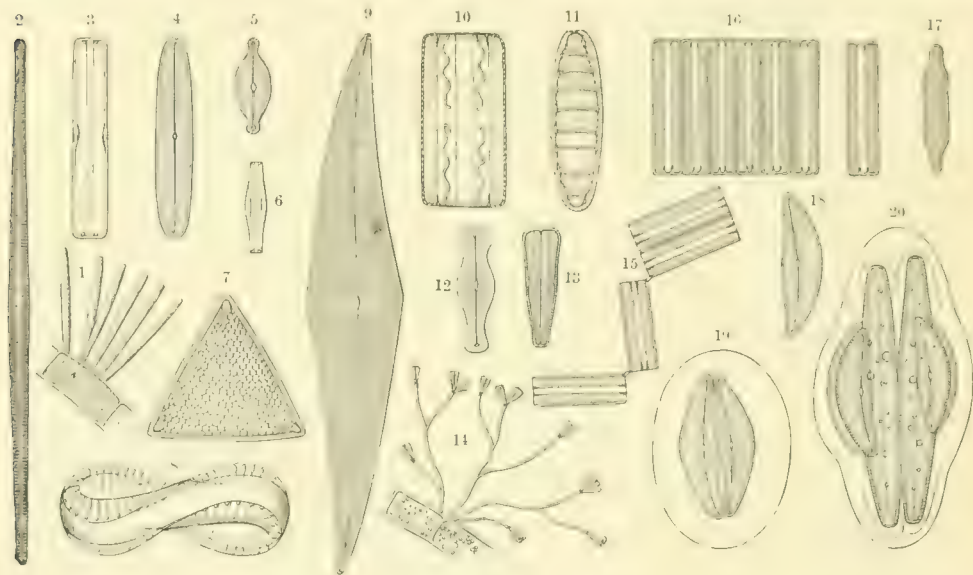


Fig. 369.—Diatoms.

¹ Several individuals of *Synedra Ulna* attached to a cell of an aquatic plant. ² A single individual of *Synedra Ulna* more highly magnified. ³ and ⁴ *Navicula Liber*, seen from the side and from in front. ⁵ and ⁶ Similar views of *Navicula tumida*. ⁷ *Triceratium Favus*. ⁸ *Campylodiscus spiralis*. ⁹ *Pleurosigma angulatum*. ¹⁰ and ¹¹ *Grammatophora serpentina*. ¹² and ¹³ Two views of *Gomphonema capitatum*. ¹⁴ *Gomphonema capitatum* on branched stalks which are attached to some algal filament. ¹⁵ *Diatom vulgare*; the cells hang together into a zigzag band. ¹⁶ and ¹⁷ *Fragillaria virescens*, showing an individual from two aspects and a row of six joined together into a ribbon. ¹⁸ *Cocconema Cistula*. ¹⁹ Two individuals of *Cocconema Cistula* inclosed in a mucilaginous envelope preliminary to auxospore-formation. ²⁰ The two auxospores have elongated, and the old cases are seen to right and left; there is no conjugation in this instance. All highly magnified.

fits under its rim, so that the Diatoms arising in this way become smaller and smaller till a certain minimum is reached. When this diminution has gone on for a certain period an enlargement is attained by the formation of what are termed *auxospores*. The contents of the cell gather themselves together, they become free from the valves, enlarge, and then put on new valves. In other cases an actual conjugation takes place, two individuals uniting into an auxospore; or each may divide into two daughter-cells, which fuse in pairs, forming two auxospores. Fig. 369¹⁹ shows two cells of *Cocconema Cistula* embedded in mucilage previous to auxospore-formation; in fig. 369²⁰ each cell has escaped from its valves, and has doubled its original length. In this instance, however, there is no accompanying conjugation.

Diatoms are very widely distributed over the globe, and occur in quantities in

the surface layers of the sea; some 30 species have been found amongst the inorganic dust of the snow-field. There are some 2000 species of living forms.

Considerable deposits of Diatoms occur in various parts of the world; of these the most remarkable is that of Richmond, Virginia, U.S.A. It is said to extend for many miles and to be 40 ft. deep. They are found in secondary, tertiary, and more recent rocks. Siliceous marl consists entirely of the tests of Diatoms. A block of such a Diatom-deposit some two cubic feet in bulk from a fresh-water lake in Australia is exhibited in the Botanical Department of the British Museum; the number of Diatoms contained in it (there are 21 different species) is estimated as exceeding 12 billions (12×10^{12}).

Class IV.—GAMOPHYCEÆ.

Sub-class I.—CHLOROPHYCEÆ, the Green Algæ.

There can hardly be a more fascinating group of plants than this, whether to the strictly scientific botanist or to the more catholic lover of nature. In the first place, the Green Algæ are among the most widely diffused of plant-forms. They grow practically in every place where enough moisture, together with light and air, are to be had. Between tide-marks on almost every coast, floating on the surface of the deep sea, covering damp earth, walls, palings, and tree trunks, sticking to the surface of leaves in the moist atmosphere of tropical forests and jungles, and inhabiting almost every river, brook, pond, ditch, or casual pool of rain-water in all quarters of the globe, are members of this ubiquitous group to be found. Nor are they wanting from more extraordinary situations. In Switzerland, Norway, and other countries where snow is more or less permanent, the bright red patches on its surface, known as "red snow", are formed by the microscopic Alga (*Sphærella nivalis*) shown in Plate I. of the first volume. Other forms, not so far removed from *Sphærella*, live in the intercellular spaces of higher plants, such as the Ivy-leaved Duckweed (*Lemna trisulca*), the Moneywort (*Lysimachia nummularia*), and others. Yet other Algæ are found inhabiting the jelly of certain fresh-water sponges in the East Indies, where they seem to live in a regular symbiosis with their hosts. But perhaps the most curious dwelling-places of all are the hollow hairs of the Three-toed Sloth (*Bradypus tridactylus*), which are inhabited by an Alga called *Trichophilus*.

In the second place, many of the Green Algæ (and among these some of the very commonest) are the most beautiful forms of life imaginable, and the main features of their structure can be made out with quite low powers of the microscope.

But perhaps the greatest claim on our interest is made by the fact that we must look among the Green Algæ not only for indications of the origin of all plant life, and of the forms from which the whole of the higher plant world arose, but also for hints towards the solution of some of the most difficult and fundamental problems with which Biologists are occupied, questions as to the real nature and origin of sexual reproduction, as to the distinction between gametes and asexual reproduc-

tive cells, as to the physiological conditions which determine their formation, and finally, questions as to the division of labour in the protoplast itself, the function of the nucleus and its relation to the protoplasm, and how far the latter can be resolved into separate, but mutually co-operative parts.

The framework of our knowledge on the former group of questions has been, and is being, built up largely from a study of the Green Algae; of the latter—and even more fundamental—we know, as yet, very little, but the same group of plants is already beginning to yield important results, and we have every reason to expect an even richer harvest in the immediate future.

We shall now proceed to a brief review of the groups into which the Chlorophyceae may be divided, mention being made of the more interesting forms in each group.

The sub-class Chlorophyceae may be defined as follows:—Thallus of very various form, one- or many-celled, coloured green by chlorophyll which is contained in chromatophores of very various shape: the green colour rarely masked by other pigments. Reproduction by motile *zoospores*, and by *gametes*, which either resemble small zoospores, and are equal in size (*isoplanogametes*), or are differentiated into two categories; first, relatively small, active male gametes—called *spermatozoids* when they are very highly differentiated—and secondly, relatively large, passive female gametes—known as *eggs* or *oospheres* when they are quite passive. The cell produced by the fusion of the bodies of two gametes is called the *zygote*, and gives rise to a new plant either mediately or immediately. When the gametes are sexually differentiated, the zygote (now called a *fertilized egg* or *oospore*) is produced only by the fusion of a male with a female gamete.

Other reproductive cells are known as *aplanospores* and *akinetes*. *Aplanospores* are formed by the protoplasm of a cell of the thallus rounding itself off and putting on a *new cell-wall*, or dividing into several parts, each of which acquires a separate cell-wall. *Akinetes* are simply single cells of the thallus, whose *original walls* thicken directly, the cells becoming separated from the rest of the thallus. These two categories of reproductive cells germinate at once to form new plants. The Chlorophyceae comprehend the following alliances:—Protococcoideæ, Siphonæ, Confervoideæ, Conjugatæ, and Charales.

Alliance VI.—Protococcoideæ.

Families: *Chlamydomonadeæ*, *Volvoceæ*, *Pleurococcaceæ*, *Endosphaeraceæ*,
Hydrodictyaceæ.

Unicellular forms, actively swimming, floating, or fixed in habit, living either singly or united into colonies.

Family *Chlamydomonadeæ*. This family consists of minute green (sometimes red) organisms which spend the greater part of their life actively swimming about in water. Several species of the genus *Chlamydomonas* are very common in stagnant water. Each *Chlamydomonas*-cell consists of a roundish mass of proto-

plasm covered by a delicate cell-wall of cellulose. At first sight the whole body appears green, but on careful examination it will be seen that the green colouring-matter is really confined to a layer on the surface of the body. This chlorophyll-layer or *chromatophore* is specially thickened at one end (the posterior end) of the body, and a small, clear, spherical body (the *pyrenoid*) is often to be seen inclosed in this thickened portion. Round the sides of the body the chromatophore is thinner, and towards the anterior end it stops, leaving a small area of colourless protoplasm to occupy the front extremity of the organism. This is in connection with another small mass of colourless protoplasm which occupies the hollow of the cup-shaped chromatophore.

A minute red speck is visible at one side of the body, situated sometimes on the surface, sometimes at the limit between the chromatophore and the central colourless protoplasm. The rotation of the *Chlamydomonas* about its antero-posterior axis, which accompanies the jerky, forward movement (*cf.* vol. i. p. 29) can be well traced by the aid of this eye-spot, which can be seen to be carried round and round as the organism turns on its axis. The means by which the *Chlamydomonas* moves are not at first sight apparent. But when the cell has come to rest, and especially if it has been killed and its protoplasm fixed with a dilute solution of iodine, a pair of very delicate protoplasmic filaments, called *flagella*, can often be seen projecting from the colourless anterior spot of protoplasm. It is by the continual lashing of these flagella that the *Chlamydomonas* is pulled through the water. The iodine will also bring into view a small spherical *nucleus*, stained dark brown, situated in the colourless central protoplasm, and will stain the neighbourhood of the pyrenoid a dark blue. This last phenomenon is due to the formation of starch by the protoplasm round the pyrenoid. The exact part played by the pyrenoid is very obscure, but there can be no doubt that it influences in some way the formation or deposition of starch by the protoplasm.

The movements of *Chlamydomonas* are often in direct relation to light, the organisms moving towards a source of light of moderate intensity. Thus if a glass vessel filled with water containing *Chlamydomonas* be placed in a sunny window, there will be a general movement of the swarming cells to the sunny side of the vessel, causing the water to become much greener on that side. There is some evidence that it is the eye-spot which enables the organism to perceive the direction from which light is proceeding. Nearly all the motile *Protozoocoidae*, as well as zoospores and gametes which are sensitive to light, possess an eye-spot, and it has been thought that the eye-spot-pigment (a substance called *haematochrome*) may act in the same way as the visual purple in the retina of the eye.

If specimens of *Chlamydomonas* be kept for a day or two in water, some of them will often be found to have divided to form daughter individuals, which still remain inclosed within the cellulose membrane of the mother. This division is preceded by the drawing in of the flagella. The protoplasm of the body then withdraws itself from the wall, and divides transversely to form two roundish masses. Each of the latter may either at once put on a cell-wall and develop flagella, or it may divide

again, so that four daughter individuals instead of two are formed. Eventually the daughters escape from the membrane of the mother, leaving it quite empty.

The process of reproduction by simple division of all the protoplasm of an individual's body into parts, each of which forms the body of a daughter individual, is an example of almost the simplest type of reproduction known. It is true that in the lower Protozoa, which have no rigid cellulose membrane, we find an even simpler type. Since the entire organism consists of protoplasm, there is nothing left of the parent individual after division has taken place. The body of the parent simply *becomes* the body of the offspring. In the type of *Chlamydomonas* we have the dead cellulose membrane representing all that is left of the body of the parent. In many of the higher Algæ, and in all plants above the level of Thallophytes, only a *part* of the protoplasm of the plant-body is used in the formation of the reproductive cells. The rest must then eventually die. But in these lower forms, where all the protoplasm of the body is used in the production of new individuals, death, as a necessary event, can hardly be said to occur.

Gametes are formed in *Chlamydomonas* in exactly the same way as daughter individuals. They are, however, smaller and have no cell-wall. In one species at least the gametes are of two sizes. Of the smaller (*microgametes*) eight are produced from a parent individual, while only two of the larger size (*megagametes*) are formed from the parent cell. In the process of conjugation a microgamete and megagamete come into contact at their anterior colourless ends, the flagella are drawn in, and a thick cellulose membrane is secreted round the bodies of both. The protoplasm of the microgamete then passes over into the space inclosed by the part of the membrane belonging to the megagamete, and completely fuses with the protoplasm of the latter. A wall is then formed, cutting off the empty shell of the microgamete. The contents of the zygote eventually divides to form two or four new individuals which escape from its membrane. In the conjugation of most species where there is no distinction in size between the gametes, a cell-wall is only acquired *after* the foundation of the zygote. This is the regular course of events in the conjugation of the motile gametes of Green Algæ.

The genus *Spharella* resembles *Chlamydomonas* in the fundamental points of its structure. The main distinction is the existence of a considerable space separating the membrane from the main body of the protoplasm of *Spharella*. This space is bridged by fine strands of protoplasm, which radiate from the central mass and end in fine branches under the membrane. The anterior colourless protoplasm is drawn out into a beak, and to the extremity of this the two flagella are attached. The flagella often pass through two very delicate cellulose tubes, which in the common species, *S. pluvialis*, diverge from the extremity of the beak, and end on either side at the membrane. In another species (*S. Bütschlii*) the beak runs right up to the membrane, and the flagella-tubes, which are short and slightly curved, lie on the outer surface of the membrane.

Spharella pluvialis is a very well-known microscopic object, being extremely common in pools of rain-water. Its protoplasm often contains a good deal of the red

pigment hamatochrome, which may almost completely mask its green colour. It was from this circumstance that it received its name of *Hamatococcus pluvialis*. Hamatochrome is even more constantly present in *Spharella nivalis*, the "red snow", whose appearance and life-history have already been described (vol. i. p. 39). *S. Bütschlii* has its hamatochrome concentrated in an eye-spot like that of *Chlamydomonas*.

The *Volvocea* differ from the *Chlamydomonadeae* in consisting of motile colonies of cells, the members of each colony being united in a common investment. The bodies of the individuals composing the colony are also joined in some genera by protoplasmic processes. The body of each individual is identical, in the fundamental points of its structure, with that of a *Chlamydomonas* or of a *Spharella*. The *Volvocea* present us with an interesting series of forms, showing a gradually increasing sexual differentiation of gametes, and, in the higher forms, an interesting subordination of the individual to the colony as a whole.

Gonium is a form in which the colony consists of (usually) sixteen *Chlamydomonas*-like cells arranged in a flat plate, which swims in a line at right angles to its surface, the flagella of the central cells of the disc projecting forwards, those of the peripheral cells obliquely outwards and forwards. All the cells are inclosed in a general mucilaginous envelope, and are joined to one another by protoplasmic processes.

Reproduction is effected by the division of the constituent cells of the colony in two planes at right angles to one another and to the plane of the colony, so that each mother colony produces sixteen daughter colonies, whose discs of cells all lie in the same plane. Meanwhile, the mother cells are separated from one another by the gradual liquefaction of the general mucilaginous envelope, and thus the daughter colonies become independent.

Formation of isogametes also takes place, but is not thoroughly understood.

Stephanosphaera is a very beautiful form, occurring especially in pools of rain-water collected in rock hollows in hilly districts. It is often found in company with *Spharella pluvialis*. The colony consists of a ring of (usually) eight *Spharella*-like cells arranged in the equatorial plane of a spherical or ovoid cellulose membrane.

When reproduction is about to occur, the constituent cells draw in the protoplasmic processes by which they are attached to the general membrane: each secretes a membrane of its own, and then its protoplasm divides in two planes to form eight (sometimes seven) daughter-cells. When these have acquired flagella they begin to swarm, and eventually escape by bursting the membrane of the mother colony.

Gametes are formed in the same way, but usually by more divisions, as many as thirty-two being sometimes produced from a single cell. In most cases all the cells of a colony divide at once to form gametes, but this is not invariably the case. Each bundle of gametes produced from a single cell breaks up, and all the gametes begin to swarm within the colony. The gametes are spindle-shaped, each with two flagella and an eye-spot. They conjugate in pairs, usually inside the general membrane, but conjugation never takes place between two gametes derived from the

same mother cell. The actual process of pairing has been fully described, and it may be taken as a type of the course of events, as it has been observed in all Algæ with isoplanogametes whose pairing has been fully investigated. Out of the crowd of gametes swarming in all directions, two approach and stroke each other with their flagella; in some cases the two separate and both become again lost in the crowd, but, when pairing is going to take place, they become firmly fixed together by their colourless anterior ends. The long axes of their bodies may then lie in one straight line, or may diverge at a wide angle. A rotation of each of the pairing gametes about its fixed anterior end now always occurs, the bodies becoming gradually approximated, so that their long axes come to lie nearly parallel. Fusion of the protoplasm follows, beginning at the already joined anterior ends, and progressing rapidly backwards till a single mass of protoplasm is formed. The four flagella still move actively, and the *Zygozoospore*, as this active type of zygote is often called, escapes from the general membrane of the mother colony, becomes spherical by shortening of its long axis, loses its flagella, and puts on a cell-wall. The protoplasm soon loses its green colour, becoming reddish, and the zygote enters on a resting period. Eventually its protoplasm divides, producing zoospores, each of which gives rise to a new colony.

The division of the cells of a colony to form zoospores or gametes begins in the evening, and is finished soon after sunrise. In dull weather, however, its completion is delayed far into the day. This dependence of the formation of zoospores and gametes upon the influence of light, if not invariable, is found very widely among the Green Algæ.

Pandorina is a fairly common form in ponds, &c. The colony consists of sixteen wedge-shaped cells arranged in a sphere, and covered by a general investment, which is of considerable density at its external surface. The apex of each wedge is directed towards the centre of the sphere, and there is little space left between the adjacent cells. The formation of daughter-colonies is similar to that obtaining in *Gonium* and *Stephanosphaera*. The young colonies escape by liquefaction of the investing membrane. Colonies of gametes are formed in the same way, but often consist of eight instead of sixteen cells, and the acquirement of flagella and liquefaction of the mother membrane takes place more slowly. Eventually the membrane of each gamete-colony also becomes liquefied, and most of the gametes swarm out into the water. A great number of mother colonies of different sizes simultaneously take part in this production of gametes, so that the water becomes filled with masses of swarming gametes of very variable dimensions. No distinct size-categories are, however, to be distinguished. Conjugation now takes place between pairs of gametes either of the same or of different sizes; with this exception, that the largest gametes do not fuse with one another. They are relatively inactive, sometimes, indeed, remaining fixed in their colonies, and are sought out and paired with by the smaller and more active individuals. Here, then, we have a most interesting stage in the evolution of sex. The largest, relatively passive, gametes may fairly be called female, while the different sizes of smaller

gametes, though not sexually differentiated *inter se*, since conjugation is apparently possible between any two, whatever their relative size, may perhaps be considered as male in relation to the largest.

It is probable that fully-differentiated male and female gametes arose from forms such as we find in *Pandorina*, by the suppression of the intermediate sizes, the smaller and more active gametes taking on the function of actively seeking out the larger passive individuals, which on their side contribute practically the whole of the stock of food required by the zygote in germination. In correspondence with this we find the chromatophore (chlorophyll-corpusele), which may be considered as the specially food-producing organ of the algal cell, much reduced and eventually functionless or absent altogether in the more highly differentiated male gametes (*spermatozoids*).

Eudorina has a colony of sixteen or thirty-two almost spherical cells considerably separated from one another, and inclosed in a general investment like that of *Pandorina*. In the production of daughter-colonies *Eudorina* resembles the lower forms of the volvocine series, but in the sexual differentiation of the gametes there is a decided advance upon that obtaining in *Pandorina*. The perfectly passive female gametes (oospheres) hardly differ from the ordinary cells of a vegetative colony, while the active male gametes (spermatozoids) are formed in bundles of sixty-four by successive divisions of similar cells. Here, then, we find the marked difference in size between the two categories of gametes brought about, as it very often is among the Algae (and, indeed, among many other plants and animals), by a marked difference in the number of divisions occurring in their respective mother-cells. The present case in which strictly comparable cells on the one hand directly give rise to eggs, and on the other divide to form sixty-four spermatozoids each, is rather extreme, but we have already met with a similar case in a species of *Chlamydomonas*.

Each spermatozoid of *Eudorina* is club-shaped, with a colourless pointed anterior end bearing two flagella and possessing an eye-spot, and a yellowish thick posterior extremity representing the (reduced) chlorophyllous portion of the typical volvocine cell. The spermatozoid bundle (male colony) escapes from its mother-cell-membrane, and swarms as a whole towards a female colony. On reaching the latter the spermatozoids get their flagella, become entangled in the thick mucilage, and rapidly separating from one another, worm their way into the female colony. Some succeed in fusing with the individual female gametes, and each zygote thus formed will eventually give rise to a new *Eudorina* colony.

A form recently discovered almost at the same time in three different States of North America, and known as *Pleodorina*, shows an important difference from the types we have hitherto been considering. Each spherical colony consists of about 128 cells, but not all of these are capable of producing daughter-colonies. This power is confined to those cells which occupy the posterior half or two-thirds of the sphere (it should be explained that the colony moves forward in relation to a definite axis). The smaller anteriorly-placed cells are thus purely vegetative in

function, and necessarily die after the reproductive cells have given rise to daughter-colonies. This is the first time we have met with such natural death among the Algae, and it is very clearly seen to be connected with the separation of the assimilative and reproductive functions. The formation of gametes in *Pleodorina* has unfortunately not yet been observed.

The remarkable and beautiful organism called *Volvox* has been known for more than two centuries, and has long been among the most favourite of microscopic objects. The purely scientific interest which it has aroused has been as great as the æsthetic admiration which it has excited. Long and animated controversies have raged on the question as to whether it was to be regarded as an animal or a plant, as an individual or as a colony of individuals. And although these questions have now lost much of their actuality through the gradual recognition by naturalists that we have absolutely no criteria by which they can be settled, there have arisen problems which promise quite as much interest and excitement for the future.

Volvox is much larger than the forms hitherto described. The colony is spherical, and possesses a single layer of cells on its surface. In *V. Globator* the sphere may be over a millimetre in diameter, but more usually its diameter is only some three-quarters of a millimetre. A particularly large specimen may possess as many as 22,000 cells (10,000 is a more usual number). Many of the cells, however, as in *Pleodorina*, are simply vegetative, and take no part in the reproduction of the colony. Usually, in fact, only a very small minority of the cells are reproductive.

The two species of *Volvox* differ from each other in a great number of points, but we have only space for a very brief description of some of the most interesting.

The cells of *Volvox Globator* are all united together by very stout processes. Each cell, which is inclosed in a separate cell-wall, possesses all the ordinary features of the *Chlamydomonas* type.

Daughter-colonies are developed from special cells, usually eight in number, called *parthenogonidia*. They are always formed in the posterior part of the mother-colony, early becoming larger than the ordinary vegetative cells. Each divides repeatedly, and forms a hollow sphere of closely-packed cells, which, after the last division, mostly acquire the characters of the adult vegetative cells, the remainder gradually increasing in size to form the reproductive cells. The young colonies then escape from the mother, apparently by pushing themselves against and making rents in its posterior wall. Subsequently the cell-membranes swell a good deal, separating the cell-bodies from one another, and the colony attains its adult size.

In other cases gametes may be formed in a young colony. About five cells (*androgonidia*), strongly resembling the parthenogonidia, divide to form discs or hollow spheres of a hundred or more spermatozooids. The spermatozooids resemble in a general way those of *Eudorina*, but are peculiar in having the pair of flagella inserted laterally at the base of the colourless beak and near the eye-spot. In the

same colonies, but a little later than the androgonidia, about thirty much larger spherical cells, the oospheres, are developed, and these are duly fertilized, but by spermatozooids derived from another colony. The zygote has a sculptured exine. Parthenogonidia are not found in those colonies which produce gametes.

Volvox aureus (= *V. minor*), the commoner form, is usually much smaller than *V. Globator*, and has rounded cells more widely separated and connected by very delicate processes. But perhaps its most striking characteristic is the very great variability in the number and distribution of the reproductive cells. The parthenogonidia, which vary in number from one to sixteen, may either occur alone or in one colony with androgonidia or oospheres, or both. Most of the sexual colonies are dioecious, though this is not always the case. The colonies containing androgonidia unaccompanied by other reproductive cells often develop very numerous (up to 1100) spermatozoid bundles, the androgonidia forming one-third of all the cells of the colony. The spermatozooids differ from those of *V. Globator* by their larger size, by their terminal flagella at the end of a shorter beak, and by the possession of a well-developed leaf-green chromatophore. We must, therefore, consider *V. aureus* as not so highly developed, in some respects at least, as *V. Globator*.

A *Volvox*-colony always swims in the direction of a given axis passing through its body, and at the same time rotates to the right or left about an axis which is inclined obliquely to the antero-posterior axis. The eye-spots of the vegetative cells are much better developed in the anterior half of the colony, and are always situated on the side of the cell nearest the anterior pole. These facts tend to support the view of the function of eye-spots in general suggested above.

Volvox stands at the head of the series of colonial (cœnobe-forming) organisms which we have been tracing, a series diverging from a *Chlamydomonas*- or *Sphaerella*-like type, and whose successive forms gradually increase in size, complexity, and sexual differentiation. *Volvox* itself has been well spoken of as "the culmination of Nature's attempt to evolve a higher organism out of a cœnobe". It was an attempt which failed, or rather which could not be carried any further than *Volvox* itself. A delicate, easily-ruptured *Volvox*-sphere could certainly not continue to exist if it were much more than a millimetre in diameter. As it is, the wall is often split, and all sorts of smaller organisms get inside, resulting in the more or less speedy collapse of the *Volvox*-colony.

But there are other series diverging from the *Chlamydomonadeæ*, and some at least of them have followed lines on which it was possible for higher and more varied plant-forms to be developed.

At the first stage along one of these lines of descent we find ourselves among forms in which the dominant phase of the life-history falls in a resting stage, either fixed or freely floating in the water. From this resting stage motile forms (zoospores), corresponding with the free-swimming *Chlamydomonas* individuals, are directly developed. These zoospores, after a short period of swarming, come to rest, often fixing themselves by their anterior end to some solid object. With little or no change in the constitution and appearance of the cell the main portion of the

life cycle is passed in this fixed condition, and cell divisions take place, the products eventually again developing flagella and being set free as zoospores. The genera *Chlorangiium* and *Physocytium* are examples of the simplest form of this type of life-history. Forms with a rather more complicated structure in the fixed stage are found in the genera *Mischococcus* (a common form on the surface of threads of the higher Algae), *Euglenopsis* (a newly-discovered American plant), and their allies. In these the protoplasm of the zoospore, after fixing itself and putting on a delicate cell-wall, pushes out the surface of its membrane away from the substratum, thus forming a tube of gradually increasing length, the apex of which is always occupied by the protoplasm. Division of the protoplasm and subsequent pushing out of the wall of the tube in different directions by the daughter-cells results in a branching of the hollow stalk, and in this way quite a considerable branching plant-body may be produced. Eventually some or all of the cells occupying the apices of the various branches of the tube acquire flagella and escape into the water as zoospores, which again settle on solid objects and give rise to new plants.

Other forms in which the cell derived from a zoospore multiplies by division, the products eventually again giving rise to zoospores, are *Schizochlamys*, *Botryococcus*, *Dictyosphaerium* and *Tetraspora*. In these, however, the immotile phase is not fixed, but forms floating colonies of various conformation. Into this topic we cannot enter further, except to remark that *Tetraspora* forms flat colonies of cells arranged in one plane and held together by the swollen mucilaginous cell-walls. Cell division takes place in planes at right angles to that of the colony. This type of colony is specially interesting, as it suggests the form of thallus found in *Ulvaceæ*, which in turn appears to lead on to the higher forms *Confervoideæ*.

Pleurococcaceæ.—More or less closely allied to the above-mentioned genera are others which do not form zoospores at all. These types with no motile phase in their life-cycle may be conveniently classed together as *Pleurococcaceæ*. The type-genus *Pleurococcus* contains some of the most widely-distributed algal forms known. *P. vulgaris* forms the bulk of the green coating of damp earth, tree trunks, palings, &c., in all regions of the globe. It consists of roundish cells, dividing in three directions in space and thus forming solid masses of cells hanging together in multiples of two, and often flattened by lateral contact. Each cell contains several parietal chromatophores which may, however, fuse together to form a single one. Resting akinetes are formed by the cells ceasing to divide, becoming spherical, and thickening their walls. At the same time oil appears in the protoplasm. It is probably mainly in this phase that *Pleurococcus* gets distributed by the wind from one place of growth to another. Owing to the resemblance of the akinetes of some of the confervoid Algae to those of *Pleurococcus*, it has often been stated, and indeed is still held by some algologists that *Pleurococcus* itself is merely a growth-phase of these higher Algae. But recent culture-experiments leave little room for doubt that *Pleurococcus* is a perfectly autonomous form, although it may often be associated with pleurococcoid stages of other Algae. *Eremosphaera* is a pretty form, common in fresh water, with single floating spherical cells. Each cell contains numerous separate chlorophyll-

bodies, embedded in a parietal layer of protoplasm, and a nucleus suspended by protoplasmic strands in the centre of the cell. Multiplication is effected by division of the protoplasm into two daughter-cells which escape by rupture of the mother-cell membrane. *Scenedesmus* is another motionless floating fresh-water form. It consists of oblong cells united into groups of two, four, or eight, which lie side by side, palisade fashion. Some or all of the cells often possess straight or horn-like projections of their walls, which give the cell groups a very characteristic appearance. The single solid chromatophore occupies nearly the whole cell cavity. *Chlorella* is a genus whose cells are symbiotic with *Radiolaria* (yellow cells). Other forms live in a similar relation with certain Coelenterates and Platyhelminths. Several help to form lichens. Since the various genera of *Pleurococcaceæ* differ thus very widely in the form and structure of their cells, and indeed are only united by the negative character of the absence of zoospores, it is almost certain that they cannot be considered as forming a natural group. The various genera are very probably allied to different neighbouring groups from which they have been derived by the suppression of the habit of forming zoospores.

The *Endosphæraceæ* are a small and very natural group of unicellular Algæ, characterized by their habit of living in the intercellular spaces of various higher plants. They possess motile zoospores, or gametes, or both, but the motionless cells produced from these do not undergo vegetative divisions. Very possibly they represent a separate line of descent from the Chlamydomonadeæ, a line of descent in which the motionless cell has become the dominant phase in the life-cycle, and has been specially adapted to the new conditions of life, but differs from the motionless cells of the "Tetrasporaceæ" in directly forming zoospores without undergoing purely vegetative divisions.

Two forms of *Endosphæraceæ* may be taken as illustrations of this type of life-history.

Chlorochytrium Lemnæ inhabits the intercellular spaces immediately under the epidermis of the leaves of *Lemna trisulca* (the Ivy-leaved Duckweed). Each plant consists of a single, thick-walled, oval cell with a parietal chromatophore containing numerous pyrenoids and a large central vacuole. Very numerous pear-shaped isogametes are formed by successive divisions of the protoplasm of the cell. Then a layer of substance outside the mass of gametes (probably the ectoplasm of the cell) begins to swell strongly, and bursts not only the cell-wall but also the superincumbent tissue of the Duckweed leaf, forming a sphere of mucilage in which the gametes begin to swarm and to conjugate in pairs. Spherical zygozoospores are thus produced; these escape from the mucilage, and after some free swarming in the surrounding water, settle on the boundary between two epidermal cells of a Duckweed leaf, draw in their flagella, put on a cell-membrane, and form a definite parietal chlorophyll-body with a single pyrenoid. After two or three days a delicate, colourless tube is put out, which forces its way between the two epidermal cells of the leaf, and reaches an intercellular space. The contents of the zygote slowly pass over into the apex of this tube, which gradually increases in size and assumes the

characters of a young vegetative cell, the original zygote-wall remaining on the surface of the leaf as a mere cellulose knob.

The generations rapidly succeed one another during the summer months, the last-formed cells of the season becoming packed with starch grains and passing the winter in this state. These resting cells can withstand desiccation, in case the pond in which the duckweed lives becomes dried up.

Phyllobium dimorphum forms large immotile cells between the tracheids of the vascular bundles in the leaves of the creeping Moneywort (*Lysimachia nummularia*). This plant lives in damp woods and other shady places. The Rhine plain in the neighbourhood of Strasburg, where *Phyllobium* was first found in the leaves of the Moneywort, is usually flooded during the month of June, partly by the rising of the river, and partly by the thunderstorms which usually occur about that time of the year. The *Phyllobium*-cells take this opportunity to form their gametes, which are of two distinct sizes, each cell producing gametes of one size only. After the escape of the gametes into the surrounding water conjugation occurs. The zygozoospores produced have only two flagella, the body and flagella of each microgamete being completely lost in the megagamete, just as the body of a spermatozoid is completely lost in the substance of the egg. After coming to rest on the surface of a *Lysimachia* leaf, and acquiring cell-membranes, the zygotes put out delicate tubes which enter the stomata of the leaf. If a leaf is infected by a few zygotes only, the tubes formed reach the vascular bundles, and forcing their way between the elements of the wood, grow forward in the bundles, branching when they branch, and attaining to a considerable length. Eventually, towards the end of the summer, the protoplasmic contents of each tube becoming concentrated in one spot, this part of the tube swells and is cut off from the remainder by the formation of transverse partitions. The swollen part of the tube thus forms a large cell which rests during the winter, and in the next summer will produce gametes. If, on the other hand, the leaf is infected by a large number of zygotes, most of the tubes never get any further than the intercellular spaces immediately under the stomata. In this position they form small resting cells in large numbers. These eventually form *zoospores*, which apparently behave, on germination, just like the zygozoospores. The dimorphism of the resting cells of *Phyllobium* thus depends directly on the *amount of space* at the disposal of the germ tubes. This conclusion can be confirmed by cultivating the germ tubes apart from the leaves of the host.

The purpose of the germ tubes of *Chlorochytrium*, *Phyllobium*, and their allies in penetrating the leaves of their hosts, seems to be simply that they may gain the advantage of a quiet protected place for their development. Just in the same way Diatoms and other unicellular forms often live comfortably in the empty cells of Algæ, the intercellular spaces of the Bog-moss (*Sphagnum*), and similar situations. Only in the case of these Endosphærææ the association of the Alga with its habitat is invariable and adaptive, not merely casual and unrelated. But the Endosphærææ are not parasites in any sense. They take no food from their "hosts" nor do they exercise any appreciable influence on the latter. This is sufficiently proved by the

fact that *Lemna trisulca* lives quite happily and can flower when infested with *Chlorochytrium*, and that the germ tubes of *Phyllobium dimorphum* usually enter dead leaves of the Moneywort. Another form which always enters the living leaves of a river-weed, continues its course of development whether the leaves die or remain alive. It is not, however, difficult to imagine how a form like *Phyllobium*, living as it does in the vascular bundles of its host, might acquire a parasitic habit by tapping the food supplies. As a matter of fact certain confervoid Algae are known whose presence results in the death of the leaves they inhabit, though probably not by direct appropriation of the food of the host.

Resembling the *Endosphaeræ* in possessing motionless cells which form zoospores but do not undergo vegetative divisions, are certain common fresh-water forms of which *Characium* and *Sciadium* may be mentioned. A plant of *Sciadium* originally consists of a single cylindrical cell whose contents breaks up into zoospores. These zoospores have acquired the peculiar habit of settling on the rim of the mother-cell, instead of seeking out fresh spots for their development. Each zoospore produces a single cell like the mother, so that a whorl of cells of the new generation is formed on the top of the original cell. This process may be repeated for two or three generations, after which the zoospores will settle on some other object and start fresh "plants".

The *Hydrodictyaceæ* are a group of Algae which form immotile colonies. The cells of these colonies resemble the single cells of the forms we have just been considering in producing zoospores or gametes, but undergoing no vegetative divisions. The colony is formed by the joining together in a definite way of the group of zoospores formed in a single cell of the mother-colony. Each of these zoospores then develops into an adult vegetative cell.

The recently discovered genus *Euastropsis* (so called from its likeness to the Desmid *Euastrum*) is the simplest type of the family. It consists of two mitre-shaped cells joined to one another by their bases. Each cell contains a parietal chromatophore with a single pyrenoid, and a single nucleus. The contents breaks up by successive divisions into 2-32 zoospores, which escape from the cell surrounded by a general membrane. After oscillating for about a quarter of an hour, the zoospores become attached in pairs by their anterior ends. Each pair then takes on the characters of the two-celled colony.

Pediastrum (fig. 370⁶) consists of a disc of cells, of which the marginal ones are often drawn out into lobes or processes. The chromatophore is parietal with a single pyrenoid; there are numerous nuclei. The formation of zoospores is like that of *Euastropsis*, but their movement is more lively, and eventually all the zoospores formed in a single cell join together to form a new *Pediastrum*-colony (figs. 370⁷ and 370⁸). Gametes are formed in the same way as the zoospores, but are smaller and more numerous. They escape from the investing membrane, swim freely in the water, and fuse in pairs to form zygotes. From these zygotes new *Pediastrum*-colonies are produced indirectly, probably by a method like that obtaining in *Hydrodictyon*.

Hydrodictyon, the Water-net (figs. 370¹ and 370²) is a beautiful organism forming net-like colonies of cylindrical cells, which are joined end to end, forming the sides of the polygonal meshes. Each cell may be as much as 1 centimetre in length. A thin layer of protoplasm containing numerous small nuclei lines the wall and incloses a large central vacuole. The chromatophore, or chlorophyll-layer of the protoplasm, contains many pyrenoids, each surrounded by a sheath of starch grains. Fine-grained starch is also scattered through the substance of the chro-

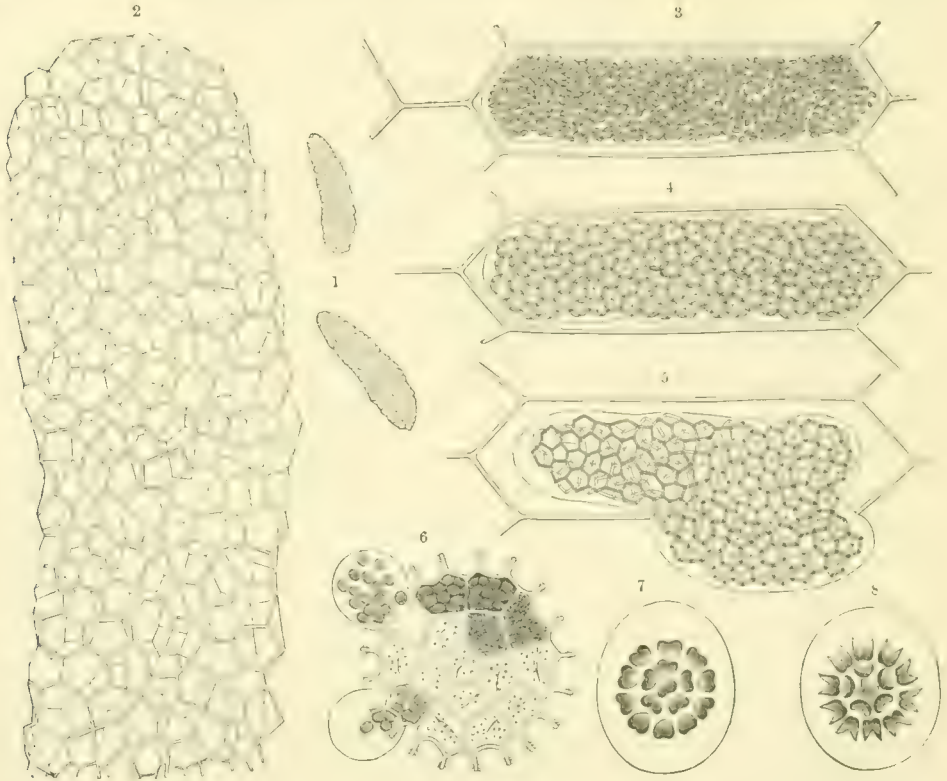


Fig. 370.—Hydrodictyceae.

¹ The Water-net (*Hydrodictyon utriculatum*), nat. size. ² A portion of the same magnified 50 diameters. ³, ⁴, and ⁵ Formation of zoospores in a cell of *Hydrodictyon*, showing their union together, and escape as a young net; $\times 300$. ⁶ *Pediatrum granulatum*; development and escape of zoospores, the lightly-dotted chambers already vacated. ⁷ and ⁸ Zoospores after their escape arranged as a new *Pediatrum* plant; $\times 240$.

matophore. This stroma-starch appears in great quantity when growth is checked and assimilation remains active, disappearing again if assimilation is stopped. The pyrenoid-starch, on the other hand, seems to be withdrawn from the ordinary metabolism of the cell, since it is formed round each pyrenoid early in the life of the cell, and remains there under all circumstances, unless the cell is on the point of actual starvation in the dark, till the onset of reproduction. When zoospores are about to be formed the pyrenoids together with their starch disappear, and abundant stroma-starch appears. At the same time the nuclei multiply a good deal by division, and eventually the whole of the protoplasm divides to form a great num-

ber of zoospores. These zoospores, however, never become free like those of *Pediastrum*, but remain joined together by strands of protoplasm, and after a certain amount of shifting backwards and forwards, come to rest with their ends in contact. Each then gradually assumes the characters of a *Hydrodictyon*-cell, the young colony eventually escaping from the mother-cell (figs. 370³, 4, 5). Gametes are formed in the same way as zoospores, but are smaller and more numerous. The spherical zygote gradually increases in size, and its contents breaks up into 2.5 large zoospores, which develop into large cells with pointed processes, the so-called *polyhedra*. In the interior of each polyhedron an embryonic *Hydrodictyon*-net is developed from swarm-spores, and in the cells of this ordinary *Hydrodictyon* colonies are found.

It has been shown experimentally that any *Hydrodictyon*-net above a certain size and age is capable of producing either zoospores or gametes, and that the stimulus to the formation of one or the other is given by external conditions. Thus bright light, fresh water rich in inorganic nutritive salts, and fairly high temperatures, are favourable to the production of zoospores, while the reverse of these conditions, and especially the presence of organic substances, such as sugar, tend to make the cells of a net produce gametes. The conditions favourable to zoospore-formation are also of course, favourable to active vegetative growth, and no doubt the abundant formation of new protoplasm is a necessary preliminary to the production of zoospores. A slight check to the processes of assimilation and growth is apparently necessary in order to give play to the zoospore-forming forces. Thus, experimentally, a change from a strong solution of nutritive salts to fresh water will induce the formation of zoospores in nets which would simply have gone on growing if left in the nutritive solution. A similar check is probably given by the waning light in many Algae in which zoospores are produced at night. For the production of gametes, on the other hand, an actual reversal of the conditions favourable to growth is necessary. In nature this probably happens when by very active growth the whole of the water of a pool is filled with nets, the inorganic food and oxygen are exhausted, and the normal chemical processes of the cell receive a check. The formation of gametes and zygotes under these conditions is obviously adaptive, since the zygote can, although it need not, rest during several months till the conditions are quite altered. We may therefore conclude that, whereas zoospores are especially designed to multiply and distribute the species, zygotes are intended to preserve it under unfavourable conditions. It is probable that the production of large zoospores and polyhedra is a necessary part of the life cycle following the germination of the zygote, and cannot be altered by the incidence of different conditions.

Alliance VII.—Siphonæ.

Thallus consisting of a tube, often much branched, and containing many nuclei. This tube is the production of a single cell, but in the more complicated forms is often shut off into compartments by transverse septa. Reproduction by zoospores

and planogametes, or spermatozoids and eggs: in very many forms no reproductive cells are known. The higher forms of Siphonaceæ often produce plant-bodies of very definite and characteristic external form, and of considerable size. In some cases these simulate the external form of various higher plants.

Families: *Botrydiaceæ*, *Phyllosiphonaceæ*, *Vaucheriaceæ*, *Bryopsidaceæ*,
Caulerpacææ, *Codiaceæ*, *Valoniaceæ*, *Verticellatæ*.

Botrydiaceæ.—*Botrydium granulatum* is a little plant found growing especially on loam at the damp edges of ponds and ditches. It consists of a club-shaped or balloon-shaped green shoot-portion, about 1-4 millimetres in diameter, continuous with a simple or branched tubular colourless root-portion which is embedded in the substratum. The entire plant consists of a single cell, that is to say, its cavity is continuous throughout. The wall is lined with a thin layer of protoplasm, which contains many nuclei, and, in the shoot, a net-like chlorophyll-layer.

Botrydium can reproduce itself in very various ways, according to the incidence of external conditions. The simplest form of propagation is by budding, which takes place under conditions favourable to the ordinary vegetation of the plant. The shoot-portion of a small vegetative plant sends out a process which swells to the size of the mother shoot, puts out a colourless root, and is then constricted off to form a separate plant. But if the plants are covered with water they cannot go on growing comfortably, and accordingly the protoplasm breaks up to form a number of zoospores, each with a single flagellum and two lateral chromatophores. The mass of zoospores is subjected to considerable pressure by the swelling up of a ring-like area of the wall, and the tension becomes so great as to rupture the wall in the centre of the ring and expel the mass of zoospores into the water. On damp soil the zoospores come to rest, and germinate to form new plants. If a zoospore cannot escape from the water it enters on a resting stage, which gives rise to a new plant directly it finds itself on damp soil. Further, if a young plant is exposed to bright sunlight, its protoplasm breaks up into a number of spherical cells, each of which puts on a cell-wall. If now these spherical cells (*gametangia*) are placed in water, the contents of each breaks up into spindle-shaped, biflagellate gametes, which conjugate in pairs to form zygotes. These zygotes can rest for a longer or shorter time, but if placed on damp earth they at once germinate to form new plants. If, on the other hand, the gametangia are placed in water after being kept for two years they give rise to biflagellate cells which rather resemble the gametes, but which on damp soil germinate directly to form vegetative plants. Finally, if the gametangia are at once placed on damp soil, their contents does not break up, but the whole gametangium germinates and produces a plant. Supposing a large *Botrydium*-plant, with a balloon-shaped shoot, be exposed to insolation (bright light) its contents, instead of forming gametangia, travels down into the root, and the protoplasm there divides to form rows of *root-cells*, each with an independent cell-wall. If a root containing root-cells be placed in water, the protoplasm of each cell breaks up into a number of zoospores: if the root be placed on damp earth each

root-cell sends out a tube which grows into a young vegetative plant: if left in the soil, the latter remaining damp, each root-cell germinates to form a peculiar thick-walled plant called a *hypnosporangium* which can withstand desiccation, and which in water gives rise to a number of zoospores.

The above facts may be briefly expressed by saying that any stage in the life-history of *Botrydium* tends (1) on damp soil to form vegetative plants, (2) in water to form zoospores or gametes, (3) in dry conditions to form resting cells. There can, then, be no doubt that here, as in the case of *Hydrodictyon*, we are justified in saying that the form which any given set of conditions tends to produce is adapted to meet those conditions.

Phyllosiphonaceæ.—*Phyllosiphon Arisari* is an Alga living in the intercellular spaces of the leaves of *Arisarum vulgare* in Southern France and Italy. Its thallus consists of a much-branched tube, the parietal protoplasm containing many nuclei and small disc-shaped chromatophores. Unlike the *Endosphaerææ*, the presence of *Phyllosiphon* has a considerable effect on its host, causing blotches of dead tissue to appear in the leaves. As the Alga can presumably assimilate quite well for itself, this destruction of tissue is probably caused by withdrawal of water from the cells of the host. The only kind of reproductive cells which *Phyllosiphon* is known to produce are aplanospores (non-motile spores). These are formed by the division of the whole of the protoplasm of the thallus. They are extruded by the swelling of the inner membrane of the tube which bursts the outer membrane just under a stoma, shooting out a jet of mucilage in which the aplanospores are embedded. The latter germinate directly, the germ-tubes entering the leaf between two epidermal cells.

Vaucheriaceæ.—This family includes only the well-known and widely distributed genus *Vaucheria*. Different species of *Vaucheria* grow in brackish and fresh water, both running and stagnant, or in the air in damp situations. The thallus consists of relatively coarse branched tubes, quite visible to the naked eye. The interior of the tube is lined by a layer of protoplasm containing numerous disc-shaped chlorophyll-grains and many nuclei. The *Vaucheria*-plant is fixed to its substratum by short-branched, colourless processes, but, except in connection with the formation of reproductive cells, transverse septa are not formed in the tubes.

The gametes of *Vaucheria* are formed in special organs, known as antheridia and oogonia. The distinction of sex is very strongly marked, the male gametes or spermatozooids being very small oval cells, each with two laterally inserted flagella, while the female gametes or eggs are very large and quite motionless. The antheridia are often spirally curved branches of the main tube, a transverse wall separating the upper part of the spiral, the antheridium proper, from the lower part, which is continuous with the cavity of the vegetative tube. Sometimes, however, the antheridium is straight and club-shaped, and in other cases it may be separated from the main tube by an intermediate cell. The thirty-five species of *Vaucheria* are classified according to the characters of their antheridia. The oogonia are

ovoid or spherical, and usually possess a lateral beak. While the antheridium produces a large number of the small spermatozoids, the oogonium gives rise to a single large egg. An account has already been given of the process of fertilization (see p. 58, and figs. 204⁵ and 204⁶, on p. 53).

Vaucheria also produces peculiar zoospores, whose development and subsequent behaviour have been described on pp. 23 and 24 of vol. i. (see Plate I. a-d). The cilia with which the surface of the zoospore is clothed are arranged in pairs, and in the colourless external layer of protoplasm just below each pair of cilia is situated a single nucleus. This suggests that the zoospore of *Vaucheria* is to be regarded as really equivalent to a great many zoospores which have not separated during development, each nucleus, with its pair of cilia and a certain amount of chlorophyll and protoplasm, representing an ordinary zoospore. It has been found that if, as often happens, the zoospore breaks into two during its struggles to escape from the end of its tube, the front part rounds itself off and swims away, behaving just like an entire zoospore. In some species of *Vaucheria* the zoospores are only partially clothed with cilia and come to rest soon after their escape. In yet others they have no cilia at all, and either escape by dissolution of the end of the tube, or germinate *in situ*. Here then we have a transition from the formation of active zoospores to the production of passive aplanospores.

The occurrence and form of reproduction is here even more entirely under the control of conditions than is the case in *Hydrodictyon*. The age and size of the plant are no longer factors, since sexual organs and zoospores can be formed on quite short germ-tubes. Cultivation of the plant in a solution rich in inorganic food-salts always gives it a tendency to produce zoospores, but the immediate stimulus to their formation is given by a distinct *change* in the conditions, just as is the case in the Water-net. In *Vaucheria* this change is especially necessary, since each zoospore is formed in the apex of a tube, and apical growth must be stopped in order to allow free play to the zoospore-forming forces.

The nature of the change, so far as regards the medium, is apparently immaterial—it may be a change from running water to still water, or from a damp atmosphere to water, or in the temperature or concentration of the culture-solution, but it is a change from light to darkness which is especially effective. This is quite contrary to the case of *Hydrodictyon*. The presence of water and a temperature between 3° and 26° C. are absolutely necessary conditions of zoospore-formation.

The former condition is obviously adaptive. The formation of sexual organs is specially induced by the replacement of inorganic salts by organic substances (*e.g.* sugar), just as in the case of the gametes of *Hydrodictyon*, but antheridia and oogonia, which are formed much more frequently and easily than are the Water-net gametes, often appear in the presence of salts, and when growing in a damp atmosphere. Light and a temperature above 3° C. are absolutely necessary conditions.

The most striking point in the physiology of the reproduction of *Vaucheria* is the prominent part played by the sexual organs. These are undoubtedly the principal means of propagation the plant possesses, the zoospores, which usually fulfil this

role, having fallen to a subordinate position. Only in forms like *Vaucheria clavata*, adapted to life in rapidly-flowing water, have the zoospores a primary importance. Sexual reproduction is here difficult, and zoospores are always produced in abundance on the slightest change of conditions.

Bryopsidaceæ.—This family consists of marine, mostly tropical, forms. The plant-body of *Bryopsis* has quite a definite form, and consists of a tube forming the main axis, fixed below by short root branches, and bearing above in acropetal succession a series of branches, some of unlimited, some of limited growth. In these latter are formed swarming cells which are of two sizes, the smaller being yellowish, while the larger have each a green chromatophore. It seems very probable that these are anisogametes, but their conjugation has not been observed.

Derbesia is a genus like *Bryopsis* in many respects, but with special zoosporangia which produce curious zoospores, each with an anterior crown of cilia.

Caulerpacææ.—The genus *Caulerpa* contains nearly one hundred species, which present the most varied external forms, simulating those of many of the higher plants, such as Mosses, Ferns, Mare's-tails, Cactuses, Conifers, &c. Each plant, however, consists simply of a single much-branched but uninterrupted tube, the branches taking the forms of roots, leafy shoots, &c. The tube is supported internally by a complicated system of "beams" of cellulose which run out from the walls.

The *Caulerpas* live mainly in tropical and subtropical seas. They often grow together in large masses, forming great beds of sea-weed, their creeping stems or "rhizomes" extending many yards. No reproductive cells have as yet been found in any of them, multiplication taking place apparently solely by the breaking off of parts of the thallus, which drift and fix themselves elsewhere.

Codiaceæ.—Under this name we may conveniently place together a group of forms specially characterized by a thallus consisting of richly-branched tubes, which are interwoven to form a mass of more or less solid character, which possesses in each genus a definite and characteristic external conformation. Thus, *Penicillus* has a long cylindrical "stalk" fixed below by "rhizoids" and bearing above a head of free dichotomously branching radiating filaments. The older parts of the stalk are strongly incrustated with calcium carbonate.

Udotea has a stalk often creeping and branching, bearing flat fan-shaped fronds. Spherical bodies, the nature of which is unknown, are borne on short side branches of the tubes of which the frond is built up. *Halimeda* possesses a thallus mainly composed of series of heart- or kidney-shaped segments, which give many of the species the appearance of an *Opuntia*. There is usually a considerable deposit of calcium carbonate covering the thallus. Roundish structures, produced in grape-like bunches on the edges of the segments, liberate swarming cells whose behaviour has not been followed.

Codium has no well differentiated stalk or segments; the thallus is very various in form, and is differentiated into a well-marked pith and cortex, the tubes being mainly longitudinal and loosely packed in the former, while the latter consists of club-shaped closely-packed branches arranged at right angles to the surface. In

certain branches of the latter swarmers of two sizes are produced. Analogy would lead us to suppose that at least the smaller of these are gametes, but their behaviour has not been observed. Some species of *Codium* (e.g. *C. tomentosum*, with a dichotomously branched furry thallus) occur on our own coasts. The remaining Codiaceæ are largely tropical, but very widely distributed.

Valoniaceæ.—We may include in this family an assemblage of genera whose thallus consists of a branching tube, usually forming transverse walls, but with no interweaving of the branches such as we get in Codiaceæ.

The simplest type is found in *Valonia*, a form which at first consists of a single club-shaped cell, which produces a whorl of branches at its upper end. Each of these may again produce a whorl of branches of the second order.

A group of very beautiful genera form leaf-like structures, the branching of the thallus taking place in one plane. *Struvea* consists originally of a single cell, which grows apically and becomes divided by transverse walls into a series of segments. Each of these segments bears a pair of branches coming off right and left, and each branch behaves like the main axis. The secondary and tertiary branches thus produced come into contact, fixing themselves one to another by means of curious little rosette-like organs called *tenacula*, and the whole thus forms a net-like structure with larger or smaller meshes between the branches. The definite usually oval form of the "leaf", of which the main axis forms the midrib, and the primary branches the principal veins, is due to the latter, after they have attained a certain length, ceasing to produce branches on the side towards the base of the thallus, and at the same time bending forwards and inwards to join the primary branch next in front.

Struvea delicatula sometimes lives in the tissue of a Sponge belonging to the genus *Halichondria*. There is a reciprocal effect on the form of the two organisms, the Alga only taking on the characteristic *Struvea*-form when part of its thallus grows out clear of the body of the Sponge. In consequence of this it was for some time not suspected that this sponge-inhabiting Alga had any connection with *Struvea*. Neither organism seems to suffer from the association, and there is some evidence for regarding it as a case of true symbiosis.

Anadyomene is another very beautiful form resembling *Struvea* in the construction of its thallus, but with no meshes between the cells. It consists of two kinds of cells, the more elongated form the "ribs" of the thallus, the smaller and more rounded make up the intermediate tissue.

The genus *Boodlea*, in which the branching takes place in more than one plane, forms a transitional form connecting these genera with *Cladophora*, which is usually regarded as belonging to the Confervoideæ.

Verticillatæ.—In this group of the Siphonæ the thallus consists of a long cylindrical undivided stalk, fixed below by rhizoids, and bearing above acropetal whorls of simple or branched appendages of limited growth. In some of these appendages gametes may be produced; zoospores are apparently absent. It includes two sub-families, the Acetabulariæ and Dasycladæ.

Acetabulariæ.—Fertile and sterile appendages distinct. *Acetabularia mediter-*

ratnea: the lower part of the long cylindrical stalk is incrustated with calcium carbonate, and fixed to its substratum by short irregularly branched rhizoids. The rhizoid-bearing portion is called the *foot*, and below it there is a thin-walled branched continuation of the stalk, called the *basal division*. Near the apex of the stalk are borne 1-4 whorls of polychotomously branched sterile appendages, which soon fall off.

Above these is an umbrella-shaped whorl of simple appendages in lateral contact, whose cavities are not shut off from that of the stalk. The whole of the upper part of the plant dies off each autumn, only the foot and basal division remaining alive through the winter. In the spring a new shoot is produced. Apparently after several years the contents of each simple appendage of the umbrella (which may now be a centimetre or more in diameter) divides up into a number of oval bodies, each surrounded by a fairly thick wall and containing chlorophyll and starch. These are the *gametangia*. After their escape by the dissolution of the umbrella, the contents of each divides up to form a number of gametes. Considerable pressure, caused by swelling of the ectoplasm and osmotic tension in the vacuole of the gametangium, bursts off a lid at one end, and the gametes escape. Conjugation only occurs between gametes derived from distinct gametangia.

Dasycladææ.—No distinction between fertile and sterile appendages. *Dasycladus* has a single stalk-cell fixed below like *Acetabularia*, but bearing very numerous whorls of appendages, which stand so close together as to give the entire plant a resemblance to a minute fox's brush. Each appendage bears a terminal whorl of branches, and in the middle of these is a shortly-stalked, nearly spherical gametangium. The gametes conjugate, but apparently only with those from certain other plants. This fact at first led to the supposition that we had here a physiological distinction of sex in gametes, which in external appearance are all alike. This is, however, quite an unjustifiable and unnecessary assumption. We have no right to predicate sexual differences between gametes which do not show any of the well-recognized characters of male and female reproductive cells. The tendency to avoid pairing with closely related gametes, which we may call *exogamy*, is quite a distinct phenomenon, not only among isogamous Algae, but also among many of the higher plants, where it coexists with strongly-marked sex. The phenomena of self-sterility is an extreme case of this.

Neomeris and *Cymopolia* are two tropical and subtropical genera, whose thallus is very strongly incrustated with calcium carbonate. The arrangement of the branches resembles that found in *Dasycladus*, but on the ends of the younger ones hairs are borne, which serve to protect the growing apex of the plant. In *Cymopolia*, of which the main stalk branches, and the thallus attains a considerable size, these hairs are borne by simple branches produced on special constricted and uncalcified zones of the stalk. The apices of the secondary branches are in both genera swollen up, and in close lateral contact, thus forming a continuous surface on the exterior of the plant. The calcium carbonate is deposited as a thick layer underneath these swollen ends.

A whole series of fossil forms from the chalk and tertiary deposits serve to connect the various existing types of these and allied genera.

Alliance VIII.—Confervoideæ.

The Algæ included under this alliance possess a type of thallus composed of distinct and separate cells. These cells are united usually into linear series, which form branched or unbranched threads. In a few families, however, cell-division takes place in two, or even three, dimensions, resembling some *Protooccoideæ* in the formation of cell-surfaces or cell-masses. Zoospores are produced by nearly all confervoid forms. Aplanospores and akinetes are common. The gametes may be isogamous, or they may show marked sexual differentiation.

Families: *Ulvaceæ*, *Ulotrichaceæ*, *Cylindrocapsaceæ*, *Ædogniaceæ*, *Cladophoraceæ*, *Gomontiaceæ*, *Sphaeropleaceæ*, *Chatophoraceæ*, *Trentepohliaceæ*, *Mycoidaceæ*, *Coleochaetaceæ*.

Ulvaceæ.—This family is usually regarded as the lowest of the confervoid series. It is characterized especially by forming cell-surfaces instead of filaments. Zoospores with four flagella and isogametes with two, as well as akinetes, are formed in the group. *Monostroma* very much resembles *Tetraspora* among the *Protooccoideæ*, from which we may suppose the confervoid forms to have arisen in evolution. The thallus consists of a single layer of roundish or angular cells. In germination, the zygote divides to form a small hollow sphere, which splits, and extends itself to form a flat plate. At first fixed by rhizoids, the thallus later floats freely in the water. The chromatophore is a parietal plate, covering more or less of the cell-wall, and contains a single pyrenoid. Gametes (which may develop without conjugation), or zoospores may be formed in almost any cell of the thallus.

Ulva differs from *Monostroma* in possessing a thallus of two layers of cells, those of each layer dividing independently of the other. The zygote germinates to form a fixed cell thread, which later on produces the two-layered thallus. *Ulva latissima* (the Green Laver or Sea-lettuce) is very common on the rocks of our coasts near high-tide mark. It forms large green wavy fronds firmly fixed to the substratum. It is sometimes used as an article of food.

Enteromorpha is a large genus, several species of which are common on our coasts, and some in fresh water. The thallus forms a branched hollow tube, the wall of which is one cell thick. Any cell of the thallus may act as the apical cell of a branch. The apex of the branch is solid, but the cells soon round themselves off to form the wall of the tube. The gametes and zoospores resemble those of *Monostroma* and *Ulva*.

Letterstedtia is a Cape and Australian form much like *Ulva*, but with a deeply-lobed thallus. Zoospores are produced only in the cells of the lobes.

Ulotrichaceæ.—This family contains several genera common in fresh water, and some marine forms. The thallus consists of an unbranched filament of cells seldom much longer than they are broad. The chromatophore is single, parietal, and of

very various form. Zoospores are formed in most genera. Gametes, where known, are motile and isogamous. Aplanospores and akinetes are very commonly formed, under unfavourable conditions.

Ulothrix (fig. 371), the best-known genus, possesses cells of very variable length. The chromatophore, which contains several pyrenoids, is an interrupted cylinder, and may or may not occupy the whole length of the cell. When the conditions are suddenly changed, zoospores or gametes are very readily formed, the former 1-4 the latter 4-32 in a cell. According to the size of the mother-cell and the number of divisions taking place, the size of the zoospores and gametes varies greatly, the



Fig. 371.—*Ulothrix zonata*.

1 Two filaments of this plant. 2 Escape of gametes in packets. 3 Spherical packet of gametes free from the filament. 4 Separation of the gametes. 5 Gametes swimming about and pairing. 6 Products of pairing of gametes (zygotes) attached to substratum. 7-9 Zygote giving rise to zoospores. 10 Two zoospores. 1 $\times 250$; 2-10 $\times 400$. (Partly after Dodel-Port.)

only constant distinction between them being the number of flagella, which in the zoospores are four, in the gametes two (cf. figs. 371¹⁰ and 371⁵). The zoospores or gametes escape from the mother-cell through a hole in the wall. They are surrounded by a bladder derived, probably, from ectoplasm. The swelling of this in the water helps to drag them out of the cell-cavity. The tension of the vacuole of the mother-cell, which is visible among the zoospores or gametes as a smaller bladder, also assists in pressing out the mass (figs. 371^{2,3,4}). The zoospore settles on some solid object, and, after putting out a short root-process from its colourless anterior end, produces a new cell-thread. Some of the gametes develop parthenogenetically, in which case they germinate just like zoospores, but produce usually smaller and weaker plants. The gametes which conjugate (see figs. 371⁵ and 371⁶) produce zygotes which sink to the bottom of the water, and after a period of rest grow into unicellular plants, each of which forms 2-14 zoospores (figs. 371^{6,7,8,9}). These probably give rise to ordinary plants.

The asexual generations of *Ulothrix* are produced during the autumn and winter, gametes being formed in spring, and the zygote resting through the summer. This course of events differs from that obtaining in most Alge with a similar life-history. *Ulothrix* seems especially adapted to life in cold water.

Hormidium is a genus whose members grow largely on damp earth, tree trunks, &c. The chromatophore is solid, with radiating processes and a central pyrenoid. The cells of some species divide longitudinally, so as to form threads two cells broad.

Various other genera are common in fresh water.

Cylindrocapsaceæ.—*Cylindrocapsa* forms unbranched threads of short cells with very thick walls, each thread being fixed in the young state by a cellulose foot. The gametes show a considerable sexual differentiation. The males are pear-shaped, elongated, yellow, with two flagella at the anterior end. They are produced two in an antheridium, which is formed by the division of an ordinary cell into two or four. The protoplasm of an ordinary cell rounds itself off directly to become an egg, the wall swelling and bursting at one side to allow of the entrance of the spermatozooids. Parthenogenesis also occurs.

Ædogoniaceæ.—*Ædogonium* has a thallus consisting of an unbranched thread, of rather long cells, of which the basal one is fixed to some solid object. The chromatophore often forms a continuous parietal layer containing several pyrenoids. All the cells, except the basal one, are capable of division. When division is going to occur a rim of cellulose is formed inside the cell close to the upper transverse wall. After the nucleus has divided, and the new transverse wall is formed, the rim is opened, as it were, by a circular cut from without, and the tension of the cell causes a pulling-out of the substance of the rim. The result is the intercalation of a new cylindrical piece of cell-wall in the upper daughter-cell. The young transverse wall now moves up to the lower edge of the intercalated piece of membrane. The latter soon acquires the ordinary thickness of a side wall, but the segment of the old cell-wall above the spot at which the rim was formed remains projecting beyond the new piece like the eaves of a house beyond its side walls. After the cell has divided again, another projecting piece will be left in the same way, and the series of eave-like projections so formed are a very characteristic feature of the cells of an *Ædogonium*-thread. The zoospores of *Ædogonium* are formed singly in the cells of a thread. The entire cell-body, with the exception of the ectoplasm, rounds itself off and escapes from the cell by a split in the wall. An anterior circlet of cilia surrounds the colourless "mouth place," of the zoospore. In germination, the zoospore fixes itself by the mouth place, sending out short fixing processes, puts on a cell-membrane, and then grows out to form a new thread.

The gametes of *Ædogonium* are sexually differentiated.

The oogonium is formed by the swelling-up of the uppermost daughter-cell after a division. The contents round off to form a single large oosphere. Either a round hole appears in the wall, or a circular split is formed at the upper end of the oogonium, the part of the filament above rotating through a few degrees so as to

leave an opening. A certain amount of the protoplasm of the oosphere is extruded at this spot, and forms a sort of canal of mucilage, through which a spermatozoid passes in fertilization. The spermatozoids are produced one or two in an antheridium, which are short cells poor in chlorophyll, formed by the repeated division of certain cells of a thread. The spermatozoids resemble small zoospores. In some cases they are not produced directly from the cells of a thread, but the latter give rise to special zoospores called *androspores*, which escape and settle either on or in the immediate neighbourhood of an oogonium. The androspore then germinates, producing a small structure called a *dwarf male*. This consists of a very few cells, one or more of which become antheridia, and opening by a lid, gives rise to spermatozoids, one of which pierces the canal of the oogonium, and fuses with the oosphere. The oospore, which is of a red or brown colour, produces four zoospores in germination.

Bulbochate is a genus resembling *Edogonium* in its life-history, but consists of a branched thread, only the basal cell being capable of dividing. The cells bear characteristic hairs, swollen at the base, whence the name of the genus.

Species of *Edogonium* and *Bulbochate*, which are both genera of considerable size, are found in our ponds and ditches.

The next three families are distinguished from all other *Confervoidæ* by possessing more than one nucleus in each cell.

Cladophoraceæ.—*Cladophora* is a very widely distributed genus, inhabiting both fresh and salt water. A great number of species have been described, but it is doubtful whether many of the forms are entitled to specific rank.

The thallus has a very characteristic habit. It is fixed below by an elongated basal cell, and is profusely branched, sometimes forming a spherical mass. The elongated cells possess parietal chromatophores, which cover the whole cell-wall, and possess many pyrenoids. Sometimes the chlorophyll-layer is separable into distinct angular plates. There are many nuclei in the layer of protoplasm immediately within the chlorophyll.

Many zoospores are produced in each cell. The nuclei divide a good deal, the pyrenoids disappear, and the protoplasm then divides into a number of separate masses, each of which forms a single zoospore with either four or two flagella. Gametes with two flagella are formed in many species quite like the zoospores. The zygote germinates directly to form a new *Cladophora*-plant.

The *Cladophoraceæ* show on the one hand a transition to the Siphonæ, and on the other, through certain genera with unbranched thallus and few nuclei in each cell, to the *Ulotrichaceæ*.

Gomontiacæ.—*Gomontia polyrrhiza* is an isolated form which perforates the shells of various marine molluscs, such as the whelk, the oyster, the mussel, &c. The thallus radiates on the surface of the shell, and sends branches into the substance, gradually disintegrating it. Certain branches become zoosporangia or aplanosporangia; these lose their attachment to the thallus and form fresh rhizoids. The zoospores are pear-shaped, and germinate directly to form a new thallus.

Sphaeropleaceæ.—*Sphaeroplea annulina* is a curious Alga which appears occasionally on flooded fields or in other situations. Its thallus consists of simple threads of cells which are of very various length, sometimes enormously long. The side walls are thin, but the transverse walls are often thick, and both are liable to have curious thick and quite irregular projections of cellulose. The chromatophores form irregular rings at intervals, and contain many pyrenoids. There are many nuclei, and several variable vacuoles in each cell. All the cells may produce sexual organs, the threads being either monœcious or dicecious. The contents of the cells which become antheridia become yellow-red, and break up to form a great number of elongated, pointed spermatozoids. These escape through small holes in the wall. In the oogonia the protoplasm divides to form one or two series of spherical oospheres, each with a colourless spot. The oospore has three membranes, of which the outermost is folded so as to give the oospore a star-like appearance.

In germination the oospore produces 1-8 zoospores, which have a green posterior and a pale-red anterior end. Each eventually stretches itself to form a spindle-shaped cell, and a multiplication of nuclei and pyrenoids takes place before transverse divisions occur and a new *Sphaeroplea*-filament is produced. Parthenogenesis occurs, but apparently no zoospores are formed other than those produced in the germination of the oospore.

Chatophoraceæ.—This family contains forms with a branching thallus, the branches often ending in fine hairs. The chromatophore is parietal, with one or more pyrenoids. Zoospores with two or four, and gametes with two flagella are produced.

Stigeoclonium, *Draparnaldia*, and *Chatophora* are three genera common in fresh-water in this country, and all very slimy to the touch. In the first-named genus the thallus is fixed by means of a basal disc of cells, the *sole*; the branching is simple and irregular, the branches often ending in long multicellular hairs. *Draparnaldia* shows a marked distinction between axis and appendages. The axial cells are much larger, and at the same time poorer in chlorophyll than those of the branches. The branches come off in bunches, and often end in many-celled hairs. The chromatophore possesses many pyrenoids varying in number according to the size of the cell. *Chatophora* possesses a thallus whose threads radiate and branch in all directions. The whole is surrounded by a mucilaginous investment of considerable firmness, sometimes almost leathery in consistence, so that a *Chatophora*-plant has the appearance of a slimy green ball.

There are several other genera belonging to this family, many of them being epiphytic or endophytic. *Entoderma* lives in the cell-membranes of the Brown Sea-weed *Ectocarpus*.

Trentepohliaceæ.—This family differs from the last in possessing no hairs, and in forming its zoospores in special zoosporangia.

Trentepohlia is a fairly large genus containing forms mostly living in the air on damp stones and similar situations. The thallus consists of rounded thick-walled cells, and is dichotomously or irregularly branched, partly creeping, partly upright.

The chromatophores are many, disc-like, and angular, with no pyrenoids. The cell-contents is usually much marked with hæmatochrome. The zoosporangia and gametangia are usually terminal, often swollen cells. The gametes and zoospores are much alike. *Trentepohlia Iolithus*, growing on damp stones, is known as the "Violet-stone" from possessing a scent which recalls that of violets. *T. umbrina* is often attacked by lichen-forming Fungi. *T. spongophila* inhabits the jelly of *Ephydatia* (*Spongilla*) *fluviatilis* in a certain volcanic lake in Sumatra. The situation is very advantageous to the Alga, but the Sponge seems to suffer from the piercing of its tissue by the guest. *Trichophilus* is a nearly allied form which lives in the hollow hairs of the Three-Toed Sloth.

Mycoideaceæ.—These are epiphytic or parasitic forms nearly allied to the two preceding families, and probably derived from one of them. They form regular discs of cells often attached to the host by much-branched unicellular rhizoids. The disc grows by regular divisions of its marginal cells. Zoospores and sometimes gametes are formed in all or some of the cells.

Chatopeltis forms very regular discs of cells on fresh-water plants in Europe.

Mycoidea (*Mycoidea parasitica*) forms discs of cells between the cuticle and epidermal cells of Camellias, Rhododendrons, &c. in the East Indies and South America. In this position it withdraws a good deal of water from the tissue of the leaf, and this leads to the dying of the leaf-cells in a gradually increasing area round the parasite. Eventually a hole is formed right through the leaf, and the *Mycoidea*-thallus occupying a position all round the area of dead tissue continues to increase. Zoospores are only formed in the wet season, at which time alone have they any chance of swarming and germinating on the surface of the leaf. In this position primary (embryonic) discs are formed, many of which die, and others are attacked by Fungi to form Lichens, but some succeed in sending processes through the cuticle and establishing themselves below.

Coleochataceæ.—This family contains a single small genus, *Coleochæte*, which forms radiating, dichotomously branching rows of cells, usually on the surface of other plants in fresh-water. If the cell-rows are in lateral contact, a close disc is formed (*C. scutata*), if separate a looser one (*C. soluta*), or the branching may be rather irregular (*C. divergens*). The chromatophore is parietal and disc-shaped, and contains a single pyrenoid.

Zoospores can be produced in all or only the end cells of the rows. A single one is formed from each cell. In germination a new plant is directly formed.

Coleochæte is oogamous, the plants being either monœcious or diœcious. The oogonium is always formed from the end cell of a row. The cell swells and puts out a narrow tube which opens at the end, and extrudes a drop of mucilage. The protoplasm of the swollen basal part then rounds itself off. In the forms with a disc-shaped thallus, the antheridia are produced by the division into four of the members of certain cell-groups. Each daughter-cell (antheridium) then liberates a single spermatozoid. In the branching forms certain end cells form flask-shaped swellings (antheridia), which are cut off from the mother-cell by transverse walls.

Each antheridium then liberates a spermatozoid. Fertilization has not been observed, but there can be no doubt that a spermatozoid passes down the neck of the oogonium and fuses with the oosphere. Subsequently the neck of the oogonium breaks off, the oospore puts on a cell-wall, and the neighbouring cells branch so as to form a closely investing cortex of cells round the oospore. The contents of these cortical cells turn red-brown; and after a resting stage the cortex comes off, the oospore having in the meanwhile divided to form a disc of cells, each of which gives rise to a zoospore, which escapes and germinates to form a new plant.

The structure of the oogonium, and the formation of a cortex round the oospore, as well as the formation of "carpospores" by the latter, recall the simpler Red Sea-weeds, a group which some authorities consider to be derived from some form like *Coleochæte*.

The indirect formation of new plants by the products of division of the zygote, a phenomenon we have already met with in *Pandorina*, *Hydrodictyon*, *Ulothrix*, *Edogonium*, and other forms, is probably the means by which the sporophyte generation of Mosses and Liverworts arose. At first the zygote gave rise at once to spores, but later on a certain amount of sterile tissue was produced in addition, and this formed the body of the sporophyte.

Alliance IX.—Conjugatæ.

Families: *Desmidioidæ*, *Spirogyraceæ*, *Zygnemaceæ*, *Mougeotiaceæ*.

This is a very sharply characterized alliance of Green Algæ. It is indeed difficult to determine its affinities. The forms belonging to it are especially characterized by never forming zoospores, and by possessing *aplanogametes*, i.e. gametes which, instead of escaping from the mother-cell and swarming freely, never leave the cavities of the cells in which they are produced. When conjugation is about to occur the two cells (gametangia), the contents of which will form gametes, approach one another, and their walls come into contact, either directly, or by the putting out from one or both cells of a short cellulose tube. The area of wall at the place of contact breaks down, and the whole or part of the contents of each cell then fuses with the corresponding protoplasm of the other to form a zygote.

The chromatophores of the Conjugatæ, though very various in the different families, are all very different from the types met with among the other Green Algæ.

I. *Desmidioidæ*. Cell-contents and outline symmetrically arranged on each side of a given median plane which is often coincident with a more or less deep constriction. Often unicellular.

II. *Zygnemoidæ*. Cells cylindrical, without median constriction, always forming threads.

1. *Spirogyraceæ*. Chromatophores one or more, parietal, spiral.
2. *Zygnemaceæ*. Chromatophores two, axile, roundish.
3. *Mougeotiaceæ*. Chromatophore single, axile, plate-like.

Desmidioidæ.—The Desmids are a large family of fresh-water forms numbering over a thousand species. Perhaps their most favourite habitat in this country is the water which collects and stands between mosses and similar plants on imperious soils. Many of the Desmids are among the most beautiful of algal forms.

The great characteristic of the Desmid-cell is its almost invariable division into two symmetrical halves, often separated by a circular constriction (cf. fig. 372). The cell-membrane usually consists in fact of two distinct valves whose edges meet in this median plane. In cell-division these two valves are forced apart, a new cylindrical piece of membrane being intercalated between them. A transverse wall

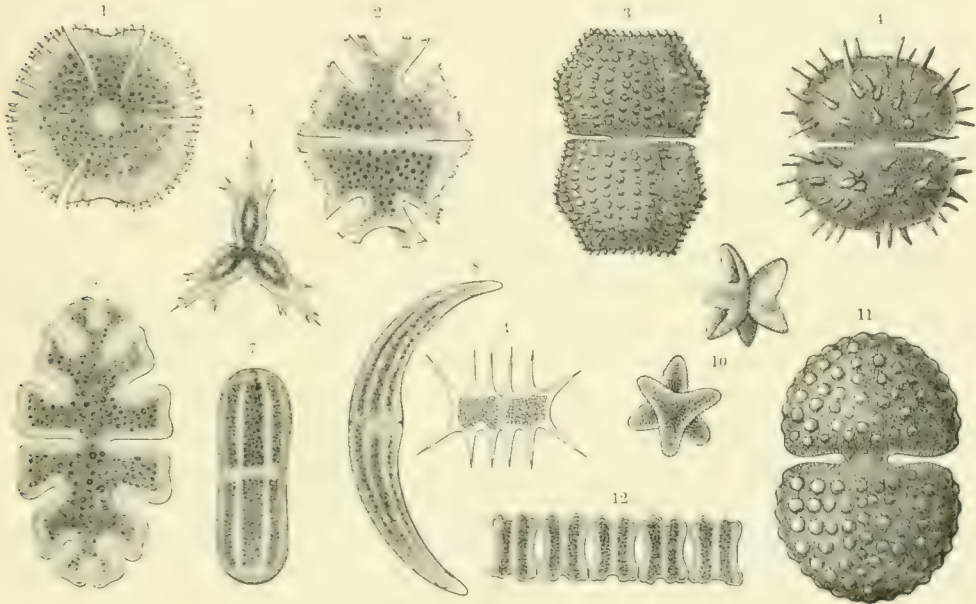


Fig. 372. Desmids.

¹ *Micrasterias papillifera*. ² *Micrasterias morsa*. ³ *Cosmarium polygonum*. ⁴ *Xanthidium aculeatum*. ⁵ *Staurastrum furcatum*. ⁶ *Euastrum oblongum*. ⁷ *Penium Brebissonii*. ⁸ *Closterium Lunula*. ⁹ *Xanthidium octocorne*. ¹⁰ *Staurastrum alternans* (two views). ¹¹ *Cosmarium tetraophthalmum*. ¹² *Aptogonium Desmidium*. All the figures magnified about 200 times.

is then formed at the equator, and each half of the new piece of wall gradually assumes the characters of the old half-cell to which it belongs.

The actual form of the cell is very various; it is often lobed, and its wall sculptured in various ways. A good idea of the shapes of some of the commoner types can be obtained by an inspection of fig. 372; see also Plate I., i, k.

The chromatophores are also extremely various in form. A common type is an axile rod bearing longitudinal plates which radiate in all directions. Each chromatophore contains one or more pyrenoids.

The cell-membrane is usually perforated by series of regularly arranged, very minute pores which give exit to extremely delicate filaments of protoplasm. The projecting end of each filament is surrounded by a mass of mucilage, and these masses together form a complete sheath covering the entire cell, and sometimes even

groups of cells (*cf.* similar phenomenon in Diatoms, p. 626). Many Desmids possess the power of locomotion. Their movement is slow and creeping, and although the means by which it is brought about are by no means fully understood, it has been shown to have a connection with the excretion of mucilage, and to stand in relation with light and gravitation. Some forms (e.g. *Closterium* and *Penium*, figs. 372^s and 372⁷) have a curious rotating movement, one end being temporarily fixed while the other moves up towards the source of light.

Conjugation takes place as already described, the conjugating cells either coming into direct contact, or putting out short tubes. The conjoined tubes are known as the *conjugation-canal*. The zygote may be formed either in this or in one of the conjugating cells. The membrane of the zygote consists of three layers, the outer one being sculptured in various ways. In germination, the outer, sculptured membrane is burst open, and the protoplasm divides to form 2-8 cells which gradually take on the characters of the adult individual.

The cells of the thread-forming Desmids (*cf.* fig. 372¹²) possess all the characters of the unicellular types, the daughter cells simply remaining together after division (which always occurs in one plane) has taken place.

Spirogyraceæ.—This family contains the single genus *Spirogyra*, many species of which are amongst the commonest Algæ in our ponds and ditches. They form green or yellowish-green slimy masses on the mud at the bottom or floating at the surface of the water. Such a *Spirogyra*-mass usually contains several species, although the bulk of it is often formed by one.

The cells of the different species vary much in diameter, from the delicate *S. tenuissima* which is only about one hundredth of a millimetre across, to *S. crassa*, which forms coarse threads as much as one seventh of a millimetre thick. Roughly speaking, the broader the cell, the greater number of chromatophores it possesses. The smaller species possess only one spiral band in each cell (Plate I., 1), the largest as many as eight or nine.

Each *Spirogyra*-cell is a cylinder, in most cases considerably longer than it is broad (though the relation of length to breadth is variable even in one and the same species), with a very delicate layer of protoplasm lining the wall, and a large central vacuole. Each chromatophore forms a band embedded in the protoplasm, and twisting spirally round and round the cell at an approximately constant angle. When there are more bands than one they cross each other at regular intervals, forming a beautiful lattice-work. In some species each band makes several complete turns in its course down the cell (fig. 373); in others, it may be inclined at such a small angle with the long axis that it makes less than a complete turn in the length of the cell. In *S. orthospira* the bands are practically parallel with the long axis, so that they do not follow a spiral course at all, but form straight bands. Each chromatophore may be isodiametric, or, on the other hand, it may form a flattened band. In the latter case its edges are usually irregularly scalloped. A single row of pyrenoids at larger or smaller intervals is found in each chromatophore.



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